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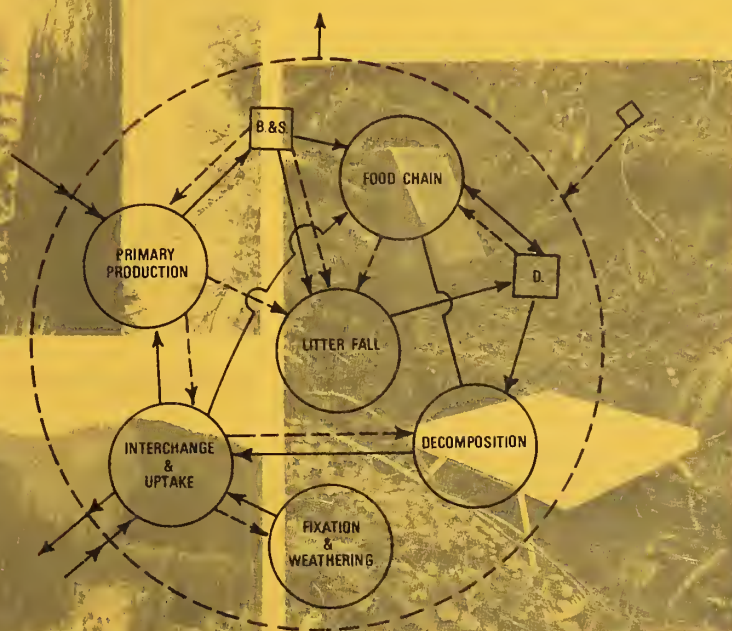
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PROCEEDINGS - RESEARCH ON CONIFEROUS FOREST ECOSYSTEMS - a symposium



THIS PUBLICATION CONSTITUTES A CONTRIBUTION TO THE
U.S./INTERNATIONAL BIOME PROGRAM

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*Research on
Coniferous Forest Ecosystems:
First Year Progress in the
Coniferous Forest Biome, US/IBP*

Proceedings of a Symposium
held at
NORTHWEST SCIENTIFIC ASSOCIATION
Forty-fifth Annual Meeting
Bellingham, Washington
March 23-24, 1972

Edited by
Jerry F. Franklin
L. J. Dempster
Richard H. Waring

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Foreword

The research program organized under the Coniferous Forest Biome is probably the largest and most comprehensive single effort at ecosystem analysis being carried out in the Western United States. After a long period of planning and discussion, it is finally in its first year of full-scale activity. Despite this youthful state there is great interest among ecologists both within and beyond the Biome "boundaries" in the conceptual basis for the Biome's program and present and planned research.

Consequently, at the invitation of the Northwest Scientific Association, members of the Coniferous Forest Biome organized the symposium, "Research on Coniferous Forest Ecosystems: First Year Progress in the Coniferous Forest Biome, US/IBP." The symposium was presented at the 45th Annual Meeting of the Northwest Scientific Association on March 23 and 24, 1972. It highlighted the concepts and plans underlying major segments of the Biome program and the numerous new insights, techniques, and data which are resulting from the varied research activities.

This volume contains the proceedings of that symposium. Publication was made possible only by the full cooperation and considerable contributions of the Pacific Northwest Forest and Range Experiment Station,

USDA Forest Service. Station staff not only assisted significantly in the editorial phases but handled the production in its entirety from edited copy to final printing. Furthermore, this was done under severe deadlines in order that the volume be available for the Fifth Assembly of the International Biological Program in August of 1972.

The editors would also like to acknowledge the numerous contributions others made to the production of this volume: To Drs. Dale W. Cole and Frieda B. Taub for their significant part in organizing and conducting the symposium; to the majority of authors and referees who cooperated magnificently in producing the necessary materials under severe time limitations; to George M. Hansen, Betty J. Bell, Mildred I. Hoyt, and others in Editorial Services of the Pacific Northwest Forest and Range Experiment Station, who bore the burden of preparing the volume for printing; and to Robert Romancier, Glenda Faxon, Virginia Hunt, James Overholser, Hans Riekerk, Charles Grier, and Laura Gregg for their part in obtaining the papers, typing, and otherwise assisting in production of the volume.

Jerry F. Franklin
L. J. Dempster
Richard H. Waring

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*Some Broader Views
of Biome Activities*

Why a Coniferous Forest Biome?

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Abstract

This introduction to the symposium outlines some of the reasons large integrated ecological research programs have been deemed necessary despite problems inherent in such "large science" programs.

The Coniferous Forest Biome program is an interdisciplinary research effort concerned with the structure and functioning of coniferous forest and associate aquatic ecosystems, particularly as they occur in western North America. Initiated as a part of the U.S. International Biological Program it is one of six biome programs organized in major biotic-environmental divisions or regions of the United States—Deciduous Forest, Grassland, Desert, Tundra, Tropical, and Coniferous Forest. The first major funding of the Coniferous Biome occurred in September of 1970, and there are now over 100 scientists from a total of 15 universities, national laboratories, and agencies involved in the program.

Many aspects of this large and vital research program will be described in papers which follow. However, questions continue to arise, such as, Is this program necessary? What differentiates the Biome efforts from the numerous existing research programs on coniferous forests, both large and small? Why has this "big science" effort been mounted?

So, before looking in detail at the Biome's research activities, I'd like to share with you some of my views on the need for and impor-

tance of the Biome program. These views are not all inclusive nor necessarily shared by all involved in the program.

To get close to home, let's consider first the increasingly complex nature of problems facing forest land managers. Questions used to be relatively simple: What cutting system will regenerate a desired forest type? What effect do different thinning or fertilizing regimes have on production of merchantable timber? What herbicides will most effectively permit reforestation and discourage brush on cutover areas? Such questions are still interesting and important. However, many of the more critical land management questions reach far beyond the relatively narrow confines of maximizing production of goods from forest lands: How do different cutting methods influence the flow and quality of water and, further, the characteristics of aquatic communities? What effect does fertilization have on the nutrient content or fertility of the water draining from the treated forest land? What happens to various pesticides when applied to the land—how fast are they degraded, where do they accumulate, and what effect do they have on nontarget organisms and the eco-

system as a whole? And, if the biological and physical questions were not sufficiently difficult (and they are), overriding economic and social considerations further compound the complexity of land management problems.

The basic knowledge of natural science required for rational resolution of some of the larger questions has thrust some new and difficult demands on the scientific community. Of course, large amounts of information are required; we often hear of an information explosion but, in fact, we are faced with a "demand" explosion—available data are totally inadequate to meet the information requirements of policymakers. More important, however, is the need for new kinds of information, particularly information on linkages between the parts of forest ecosystems, such as land and water, and between economics, sociology, and natural sciences. In effect, information is required which involves the links or relationships between the traditional units or disciplines of scientific attention and organization.

In addition to the study of linkages among different components of ecosystems, we are searching for properties that are unique to whole systems. We are asking how much time is required for an ecosystem to fully recover following disturbance, how many components are redundant in the system, what are the major selection pressures to which ecosystems respond, and finally, are we forcing ecosystems to adapt to changes faster than is possible?

It is also apparent that research programs must be planned so as to anticipate unforeseen questions and needs as well as answer immediate questions. In other words, scientists must work toward development of general principles and models which will allow us to predict from past research what will happen in a new situation which has not yet been a subject of detailed study. Examples might be the use of basic models to anticipate the effect of a cutting system in a new forest environment or of a newly developed pesticide on the animal component of a forest stand. The importance of this capability for generalization is related to another recent phenomenon, the insistence that scientists

provide immediate "best" answers to questions based on present available knowledge; society is unwilling to wait for long periods for "final" solutions.

These increased demands on the scientific community have to be met without the great increases in money and manpower experienced in the earlier postwar period. Since scientific resources are limited, they must be utilized more efficiently to meet society's needs for problem-solving information. Relevance and efficiency have become important considerations in planning and funding research programs.

In many respects, the demands outlined above run counter to the traditional ways of doing scientific research. Science has been strongly disciplinary in character with the greatest rewards going to the specialist who pursued his field in great depth. Even the applied scientist has tended to have a narrow focus looking, for example, at the effect of a cutting method on regeneration or thinning on wood yields, not at the overall effects of such treatments on ecosystems.

From another viewpoint, science has been likened to an edifice of bricks gradually built up by the effort of many individual scientists. Unfortunately, there has been a strong tendency for each scientist to produce bricks of a dimension, shape, and material primarily of interest to him. Furthermore, at least in ecology, we have lacked overall blueprints for our edifices which would provide direction as to the kinds and number of bricks we need.

There can be no questioning the need for strong basic research programs; they are essential to the advancement of science and human knowledge. Traditional viewpoints and approaches do not adequately meet a great many of today's needs, however. Consequently, the scientific community is being forced to restructure a large part of its efforts, partially from a sense of its own responsibilities and partially in response to society's pressures. Nowhere is this more evident than in the fields of natural resources and ecology. New programs are interdisciplinary efforts which try to overcome inadequacies in past research efforts. Resources are concentrated on critical areas related, either directly or in-

directly, to solution of major natural resource problems.

The Coniferous Forest Biome program is one of these integrated, interdisciplinary efforts. It has as its overall objective an understanding of how materials, such as water and nutrients, and energy enter, move through, and leave coniferous forest ecosystems, including both the terrestrial and aquatic components. The Biome program shares some common characteristics with many other large new ecological research programs: (1) It involves groups of scientists from many different fields working together toward some common goals. (2) It has a "systems" orientation; it is concerned with all parts of the ecosystem, its total behavior, and the linkages between the various components, not with a single piece. (3) Mathematical descriptions or models of the various processes, subsystems, and total ecosystem are a key to organization and synthesis of the effort. Conceptual models provide the framework for structuring the research effort and determining data needs. (4) Continuous communication between the scientist participants, including sharing of data, is an essential feature. The efforts progress via the constant interchange

between scientists, between modeling and the field and laboratory research.

In our symposium, we will try to introduce you to the kinds of research being conducted under the auspices of the Coniferous Forest Biome. The papers range widely in scope from general presentations on the conceptual basis for major program segments to results of relatively narrow research projects. Unfortunately, it is too early to provide any major synthesis of activities; this summer will be the first field season of essentially full funding. We have tried to emphasize the new concepts, techniques, and data which are emerging from the Biome's efforts. We hope that the "samples" of activities and philosophy which follow will make clearer what the Biome is trying to do and how we are going about it.

Acknowledgments

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Organization and research program of the Western Coniferous Forest Biome

An Integrated Research Component of the
International Biological Program

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Abstract

The International Biological Program was initiated in 1964. The Coniferous Biome research of the Analysis of Ecosystems component did not begin until October 1970. Other Biome programs, with the exception of the Tropical, preceded the Coniferous with the first research in the Grasslands Biome beginning in 1968. The IBP research, originally planned to terminate in 1972, has been extended in the United States through 1974. It is likely that the Analysis of Ecosystems program will be extended beyond that date in order to give the integrated research approach an adequate test.

This introductory paper describes the administrative and research organization of the Coniferous Biome and presents the broad objectives. Principal research sites and the plans for extension to other areas of the Biome are also described. As research is in the very early stages, progress can be best judged by reviewing other papers in this Symposium. Aside from accumulation of data and development of models, we have made significant contributions to the education of both undergraduate and graduate students by introducing new modeling concepts.

Introduction

The International Biological Program (IBP) began in 1964 with the specific objective of developing a world study on the biological basis of productivity and human welfare. The initiators were concerned with world-wide problems associated with increasing populations, world food supplies, changes in environmental degradation, and increasing resource use.

It was originally conceived as an 8-year program to be completed by 1972. However, because many national programs started late, IBP has been extended through 1974. There are clear indications, however, that productive research programs such as the Biome efforts will continue beyond 1974.

The nature of IBP programs and rate of attainment of specific research objectives has been variable in the many participating countries. Rate of progress has been closely related

to funds invested in the research. This discussion concerns the United States program and primarily those sections of the program under which Biome research falls. Our office will gladly supply interested scientists with references on the broader objectives and program of IBP.

The United States IBP effort has evolved as a series of large-scale, integrated research programs coordinated by a national committee (sponsored by the National Academy of Sciences) and with the financial support of the National Science Foundation (NSF).

The Integrated Research Programs (IRP's) are in two broad groups:

A. Human Adaptability

1. International study of Eskimos
2. Population genetics of American Indians
3. Biology of human population at high altitudes

4. Nutritional adaptation to environment
5. Ecology of migrant people

B. Environmental Management

1. Operating programs
 - a. Convergent and divergent evolution in the Americas
 - b. Experimental biography of the sea
 - c. Physiology of colonizing species
 - d. Atmospheric dispersal (aerobiology program)
 - e. Analysis of ecosystems
 - f. Conservation of ecosystems for scientific purposes
 - g. Chemical and biological control of organisms
2. Programs proposed but without funding
 - a. Conservation of genetic materials
 - b. Crop production under stress
 - c. Productivity and conservation of marine mammals
 - d. Nitrogen management
 - e. Phenology

U.S. IBP activities, particularly the Integrated Research Programs, provide a different focus for scientific inquiry; i.e., integrated groups of scientists working toward solution of common problems instead of individuals working alone. The changes in focus have produced some trauma and a cadre of critics. Criticisms are still abundant but help to insure better programs. Some critics say that integrated research efforts result in mediocre science, but program accomplishments must speak to this point now and in the future.

Analysis of Ecosystems and the Coniferous Forest Biome

Having dealt with generalities of the total IBP, I now wish to explain briefly some specific parts of the total research effort. As noted, the environmental management segment of U.S. IBP includes a subdivision called "Analysis of Ecosystems." This is the largest and most active U.S. IBP program. It was originally conceived by Dr. Fred Smith of the

University of Michigan, now at Harvard. The basic concepts involved are that world environments can be placed within broad units called Biomes and that integrated Biome research efforts will provide the understanding for using and conserving the resources of that environment.

Initially, the Analysis of Ecosystems program developed slowly. The Grassland Biome was organized first and has been a guide for other Biome programs. The total research effort will include the following Biomes:

Grasslands	Coniferous forest
Desert	Tundra
Deciduous forest	Tropical forest

Figure 1 illustrates the world environmental distribution of the Biomes.

The first five Biomes are now functioning. The Tropical Forest Biome is still being organized; however, NSF is supporting tropical ecosystems research by such groups as the Organization for Tropical Studies.

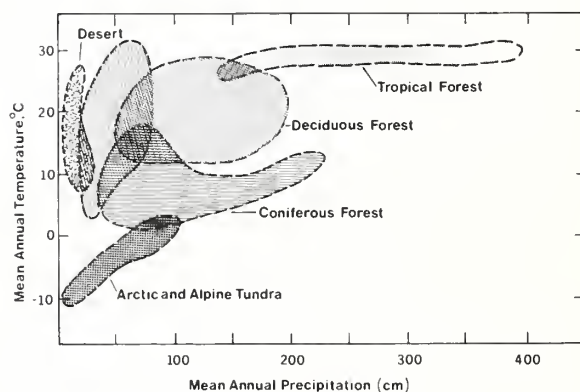


Figure 1. Distribution of Biomes.

The overall objectives of the Analysis of Ecosystems program are:

1. To establish a scientific base for programs to maintain or improve environmental quality;
2. To derive broad principles of ecosystem structure and function through an integration of the results of the six Biome studies;
3. To relate these principles to characteristics of ecosystems such as persistence, stability, maturity, and diversity; and
4. To develop and refine a generalized adaptable simulation model suitable for use in

planning studies for new development projects.

Generalized objectives of Biome research include:

1. To determine the driving forces, the processes causing transfers of matter and energy among components, the nonconcentration characteristics, and the controlling variables in each Biome;
2. To determine the ecosystem response to the natural and man-induced stresses appropriate to each Biome; for example, large herbivores in grasslands, extreme and rare weather patterns in deserts, periodic fluctuations of rodent populations in tundra, commercial use of timber in the coniferous forests, urbanization in the deciduous forests, and nutrient retention in the wet tropical forests;
3. To understand the land-water interaction characteristics of each Biome: Prairie ponds and reservoirs in the grasslands; the abundance of shallow waters in wet tundra; springs and temporary waters in deserts; river and lake systems with anadromous fish populations in coniferous forest; pollution, and eutrophication in the deciduous forest; and large river systems in tropical forests; and
4. To synthesize the results of these and previous studies into predictive models of temporal and spatial variation, effects of pollutants and of exploitation, stability, and other ecosystem characteristics necessary for resource management in each Biome.

The Coniferous Forest Biome

The history and research progress of our own Coniferous Forest Biome brings this discussion somewhat closer to home. Coincident with the development of an Analysis of Ecosystems program and the initial organization and funding of the Grasslands Biome, a large body of scientists in forested areas of the West began discussing a Coniferous Forest Biome. The University of Washington hosted the group's first formal meeting at Pack

Forest in February 1968 which produced a plan for development of a Biome research organization. The University of Montana helped to continue the discussions with a symposium on "Coniferous Forests of the Northern Rocky Mountains" held at Missoula in September 1968.

In early 1969, I accepted an invitation to become the Director of the Coniferous Forest Biome. An organizational proposal for establishment of a skeletal office and development of a Biome research program was prepared and submitted to NSF.

With these very limited funds and some financial assistance from the Central Ecosystem office and the University of Washington, and with a great deal of volunteer labor, a research proposal was prepared and submitted to NSF on December 31, 1969. The initial \$460,000 request was scaled to funds NSF had available. The proposal was approved but not funded until September 15, 1970. We are, therefore, still in the very early stages of research. Even before the first proposal was funded, a second-year proposal was prepared and this, in turn, was funded at 1.2 million dollars on January 1, 1972. We are now preparing a proposal for 1973 and 1974 with a submission date of July 1.

Coniferous Forest Biome Organization and Research

The Central Biome office is at the University of Washington's College of Forest Resources. Intensive research sites have been established on the H. J. Andrews Experimental Forest of the U.S. Forest Service in the Oregon Cascade Range and the Cedar River watershed of the City of Seattle in the Washington Cascade Range. Although many other areas had been nominated as potential research sites, these two were chosen because of their concentrations of available scientists, developed facilities, history of research, and ability to provide the types of research areas needed to accomplish the research goals of the Biome.

The total Biome research program originally called for additional coordinating sites

where validation studies could be carried out. Funds initially restricted development outside the intensive sites; however, plans for coordinating programs, sites, and activities are now being developed by the Extrapolation and Application Committee under the direction of Dr. William Laycock of the U.S. Forest Service. It appears that a diverse group of Biome-wide or coordinating site activities including: (1) major efforts to coordinate with other ongoing ecosystem research programs in the Biome; (2) cooperative studies of ponderosa pine ecosystems with the Grasslands Biome; (3) examinations of fire and disease influences on coniferous forests; and (4) validation of some initial modeling efforts will develop.

The Biome's organizational structure used in developing, organizing, and administering the research is shown in figures 2 and 3. The overall Biome research plan is developed by the Scientific Directorate, but the individual research proposals are generated by the research committees. Yearly programs develop about as follows. First, research tasks or objectives are defined. Funding guidelines for each of these are also outlined based on total

funding expected from NSF. Research committees then define specific subprogram objectives and after agreement by the Scientific Directorate, the chairman of a research committee calls for proposals from the scientific community. Proposals are reviewed by research committees and by the Scientific Directorate for task relevance and adequacy. Following revisions, deletions, and additions the proposals are incorporated into the Biome proposal. A group of scientists from other Biomes review the draft of the Biome proposal before its final preparation and submission to NSF.

Objectives of Coniferous Forest Biome Research

I will not attempt to detail the research in this brief report, but I should comment on the main objectives of all Biome research, i.e., development and validation of models of ecosystems function. The purpose of producing these models is to provide understanding of coniferous ecosystems useful for management

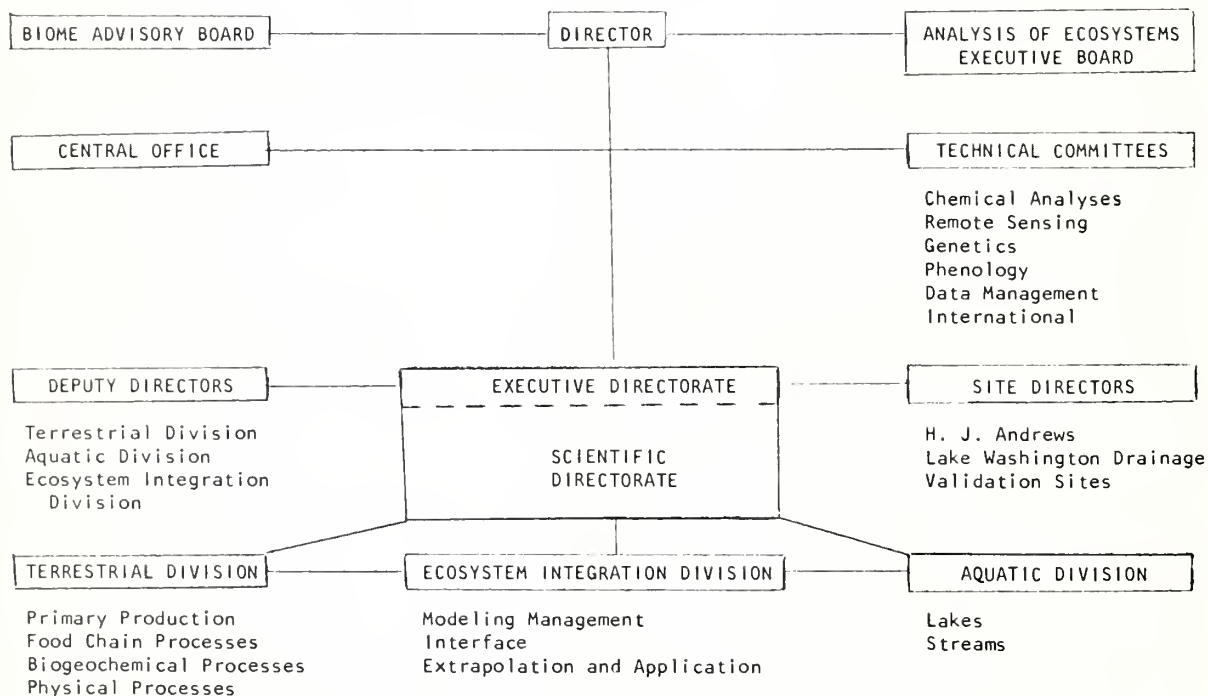


Figure 2. Coniferous Forest Biome organizational chart.

DIVISION	COMMITTEES AND SUBCOMMITTEES			
TERRESTRIAL	PRIMARY PRODUCTION	FOOD CHAIN PROCESSES	BIOGEOCHEMICAL CYCLING	PHYSICAL PROCESSES
	1. Processes 2. Biomass and Structure		1. Biological 2. Geochemical	1. Hydrology 2. Meteorology
AQUATIC	LAKES		STREAMS	
	1. Water Column Processes 2. Bottom Related Processes 3. Higher Consumer Processes			
ECOSYSTEM INTEGRATION	MODELING MANAGEMENT	INTERFACES	EXTRAPOLATION AND APPLICATION	

Figure 3. Research committees detail.

and protection purposes. The following statement by Dr. Chapman, Deputy Director for Biome modeling activity, explains Coniferous Biome modeling philosophy.

The primary aim of this ongoing research is to increase our understanding of whole ecosystems within the Western Coniferous Forest Biome; and to this aim an area of high priority is the development of models . . . with special emphasis on modeling of the aquatic-terrestrial interface.

The analysis of an ecosystem should begin by constructing models from existing data. The second step should be collection and analysis of data for testing and refining the first models. This requires participating scientists to spend considerable time thinking how their part of the system relates to the rest and about general modeling processes. As the kinds of additional data that are needed are identified, scientists will be able to conduct specific field studies designed to further improve the models. This approach establishes a continual feedback loop.

It is important, then, that participating scientists consider the understanding of systems modeling to be a major responsibility. The necessary modeling cannot be

done by, say, a systems engineer, biometrician, or biomathematician. It will not be necessary for each participant to become a full-fledged system engineer or biomathematician (although it would be highly desirable if a few did so), but it will be essential that each participant re-orient his approach and philosophy somewhat, for all should become systems modelers, in one capacity or another.

These points, made in our first proposal, can be reemphasized in other ways. In the first place, every scientific study beyond simple observation involves some type of model—verbal, graphical, or mathematical. The development of subsystem models is the responsibility of the scientist doing the substantive research and constitutes an essential part of their annual reports to the Biome. The modeling group provides support for those in need of modeling assistance and in fact has such a supportive function as one of its primary missions.

The other primary mission of the modeling group is the development of the overall ecosystem model. This is one ultimate aim of the Biome study, and while still at an early stage it will be possible to construct a total system computer model of low resolution. A better model will be achieved when reasonably sophisticated functional subsystem models

have been developed. Prior to their development the overall ecosystem model will be for the most part a translation of simple graphical and verbal models into mathematical language with many aspects of the system interpolated on the basis of empirical submodels or even crude estimates.

Ultimately both total systems models and submodels will require testing. This testing will indicate the further research needed to answer new questions or refine parts of existing models. The modeling team plays a role in assisting in the design of such new research. In this way the model building plays an essential feedback role in the program.

In addition, both subsystem models and larger ecosystem models require estimates of parameters and available data often appears inadequate. In these circumstances, it is necessary to test the sensitivity of the model to the errors of estimation. Does it make a great deal of difference if the estimates are crude? If not, the model may proceed. If it does make a significant difference, additional observations are required and further research in such areas is necessary. Obviously, such sensitivity tests cannot be made until models are fairly well developed; some models will be at this stage this year.

Specific Goals

The goal of our Coniferous Biome research is development of a basic understanding of coniferous forest ecosystems, including both terrestrial and aquatic components, so that ecological constraints on and opportunities for increased production of fiber, food, water, and wildlife can be recognized. The overall strategy includes identification of the major components and processes, both physical and organic, within the ecosystem, and definition of their interrelationships. The definition of interrelationships will be accomplished through a systems analysis and modeling program. As an overall guide for Biome research, we recognize the following general objectives:

1. To determine the major factors, both components and processes, that control the productivity and distribution of organisms

in coniferous forest ecosystems, including (a) an analysis of the structure and distribution of the principal resources, (b) definition of the functional relationships between biotic, decomposer, consumer, and producer components of the systems, and (c) analysis of the forms and degrees of stability in these systems.

2. To examine the linkage of terrestrial and aquatic components in coniferous forest ecosystems, including (a) water, energy, and transport of chemicals (including pesticides), (b) direct transport of terrestrial products into the aquatic system, e.g., through litter fall and surface erosion, and (c) return of organic and inorganic material from the aquatic to the terrestrial environment through movements of fish, birds, and insects.
3. To determine how various manipulations influence the structure and function of coniferous forest ecosystems using both unit watersheds and plot studies. Special attention is directed to the influences of manipulations on (a) stability and productivity of these systems and (b) the linkages between terrestrial and aquatic components of the systems.
4. To understand population dynamics of those major components of each trophic level which appear to influence significantly the sustained productivity and stability of various coniferous forest ecosystems within the Biome.
5. To produce models of temporal and spatial variations in coniferous forest ecosystems or system components. These models will include factors affecting productivity and stability of the systems and the linkages between terrestrial and aquatic environments, forecasting the behavior of these systems and their relationships to human manipulation.
6. To apply to specific models in the solution of major use problems in the Biome area and assist other groups or agencies to do likewise.

Since these long-term objectives provide only general guidance, considerable time and effort is spent in defining annual research tasks in order to focus the research and

modeling activities and provide a basis for phasing of the program.

The specific research tasks planned for 1973 and 1974 are to:

1. Complete initial programs in terrestrial production process measurement and modeling, using both physiological and meteorological techniques, and link results to behavior (net productivity, transpiration, etc.) of actual stands. Begin developing data for the production process models for other species and environments and for different age classes important in the Biome, including linkages of individual tree processes to behavior of stands.
2. Develop elemental cycling models of forest stand level ecosystems based upon process and transfer functions such as decomposition, ionic leaching, weathering, organism uptake, storage, and return, and meteorological and biological additions. This will include stressed systems. This fine resolution work will serve as a basis for development of unit watershed programs.
3. Begin describing paths of energy and material flow through consumers (food webs) in coniferous ecosystems under study, with particular attention to movement and accumulation of toxic materials and consequent effects of diversity, flow paths, and primary producers.
4. Complete initial nutrient, water, and energy flow models for unit watersheds and begin their refinement with particular attention to incorporation of process models. For selected compartments and transfers and in simplified form, begin examining the ability of the watershed models to describe behavior of (a) larger drainages and (b) strongly contrasting coniferous ecosystems across the Biome, and to predict (c) system responses under various stresses and over long time spans (in connection with manipulation and successional research).
5. Quantify and model paths and rates of material and energy transfers across terrestrial-aquatic interfaces, specifically including quantification of transfers in and comparisons between (a) undisturbed small streams and small lakes, (b) lakes of various topology and climate, and (c) undisturbed and clear-cut watersheds with stream systems. In the comparisons of interface transfers in undisturbed and altered systems, study consequences of terrestrial disturbances on aquatic productivity and stability with initial emphasis on stream systems.
6. Evaluate and model the trophic dynamics of four lakes of significantly different nutritional status, topology, and climate. Evaluation and modeling will be by way of three subdivisions of the aquatic system: (a) the water column, including the rapidly changing community of phytoplankton, microbes, and zooplankton, (b) the benthos, including the moderately slowly changing community of larger plants, sediments and longer life span invertebrates, and (c) higher consumers—long life span invertebrates and fish. Integrate these sub-models into a total system productivity model that allows determination of importance of various internal and external nutrient sources to lake productivity and suggests methods of management of productivity. Finally, explore opportunities for validation elsewhere.
7. Examine responses of coniferous ecosystems or subsystems to selected stresses (manipulations) in terms of material and energy flows and of productivity. This task is largely structured as validation of models and will utilize existing as well as newly acquired data. Manipulations may include (a) clearcutting, (b) fertilization, (c) addition of toxic materials (pesticides and heavy metals), (d) addition to or removal of nutrients from aquatic systems, and (e) burning.
8. Examine long-term (successional) behavior of coniferous ecosystems specifically including: (a) development of a successional model for prediction of forest composition and biomass changes, primarily by cooperation with the Deciduous Forest Biome and acquisition of necessary data base for validation of the Oak Ridge model(s); (b) descriptions of selected subsystem structures and processes across different forest age classes to test successional hypotheses regarding: (1) complexity and redundancy of detritus subsystems, (2) ratio

of gross production and respiration, and (3) conservation of nutrients within the system; (c) examination of eutrophication processes in lake systems using a series of lakes of varying "ecological stage" (nutritional status).

Each of these tasks involves an integration of efforts by several discipline groups. Expanded and more rapid interchange between discipline groups, specialists, and modelers, and between interdisciplinary units working on different levels of resolution or systems, is essential and will be pursued by all feasible methods. Expanded contact, including personnel exchange will be developed with other Biomes. Specific cooperative programs with the Deciduous Biome on succession and with the Grassland Biome on ponderosa pine-grassland systems are planned. Extension of program activities to a Biome-wide basis is essential to the 1973-74 program.

Progress

The papers presented in this symposium will indicate to some extent the progress in Biome research. Something which perhaps will not be as apparent in the presentations is our accomplishments in working together so that the total of our group research effort is greater than the sum of the individual parts. I believe some of our best progress has been in getting terrestrial researchers to consider the relationship of their work to aquatic components and how these systems interface. The same kind of crosslinks have been established among different disciplines on each campus involved in the study and perhaps even more important across state and county boundaries between different institutions. The working relationships established between scientists at Oregon State University, the University of Washington, and the U.S. Forest Service have been particularly outstanding. U.S. Forest Service scientists, especially those in the

Pacific Northwest Forest and Range Experiment Station, have made a major contribution to the success of the program.

For organizational and budget reasons we have concentrated our research effort at two major sites, the Lake Washington-Cedar River system and the H. J. Andrews Experimental Forest. We must depend upon research at these areas to provide the initial theory and models. We do recognize the broad research responsibility embodied in the term Coniferous Forest Biome and that we must expand the base by carefully choosing additional sites for study and data accumulation in order to test models and theory. We also hope that researchers will use the principal research sites to validate models they may have developed elsewhere.

We are currently engaged in a study of the entire Biome area for the purpose of selecting areas and projects which will extend Biome research in an orderly and efficient manner. We are also developing inter-Biome research efforts which will enable us to exchange models and validation studies with all other Biomes.

These remarks should serve to illustrate that the Coniferous Biome is in the early stages of a research program. Much of our effort so far has been related to organizing working groups, setting up general and specific research goals and then writing the necessary proposals. We hope the next 2 years can be devoted to the actual research and that in a similar meeting in 1974 we can demonstrate the success of the program.

Acknowledgments

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Findley Lake—the study of a terrestrial-aquatic interface [76]

P. 15-20
6020

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Abstract

The linkage of the aquatic properties of a small lake to the terrestrial landscape is under examination in the Findley Lake Basin of the Cedar River watershed. This pristine, 10 ha, oligotrophic lake is situated at 1,128 m elevation in a 162 ha watershed. During the initial year of investigation, this research program has focused primarily on a description of the ecosystem components. This initial phase of the program and the long-term objectives are discussed.

Introduction

Findley Lake is located in the upper portion of the Cedar River watershed in King County, State of Washington. Cedar River watershed is the municipal watershed of the City of Seattle and is one segment of the Lake Washington watershed which is one of the intensive study sites of the Coniferous Forest Biome, a portion of the United States International Biological Program (Gessel 1972).

A mission of the IBP is to demonstrate how sound biological information can be synthesized and used in assessing alternatives. More specifically the Coniferous Forest Biome addresses its attention to specific resource problems within the Biome. In general terms the Findley Lake interface study is directed to: better understanding of productivity and its maintenance on forest lands and adjacent surface waters; to determine the role of land and vegetation management in water quality and quantity; and to measure the interaction of animal populations upon these areas.

The City of Seattle Water Department has agreed to dedicate this entire drainage basin as a research area for the IBP, Coniferous Forest Biome program. This cooperation includes securing the timber rights of the property and developing access into the area which at the present time is by trail. The intent at Findley Basin is to maintain the pristine environment and minimize human influence while conducting the research.

Watershed Description

Findley Lake is located at 1,128 m elevation in a cirque with a maximum elevation of 1,450 m and a total acreage of 162 ha. The aquatic portion of the Findley Lake basin consists of Findley Lake proper with an area of 10 ha and two smaller ponds of about 0.4 ha each. Figure 1 defines the drainage basins of each of the ponds and lakes. Findley Lake proper intercepts 60 percent of the watershed, and the one shallow pond intercepts 14 percent. The lower, deep pond inter-

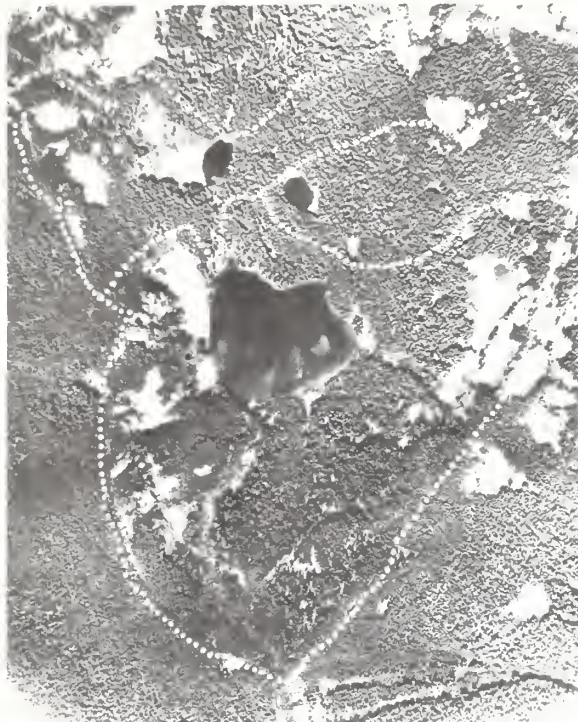


Figure 1. Aerial photo of Findley Lake basin indicating drainage basin of upper lake and two smaller ponds.

cepts each of the other two basins as well as 26 percent of the watershed directly.

The soils of the watershed have been mapped by Bockheim and Ugolini (n.d.). Many of the slopes range from 30 to 40 percent; widespread talus accounts for 16.2 percent of the total basin. Soils of mixed materials are divided as forested, semiforested, and nonforested; they account for 56.2, 4.3, and 1.6 percent, respectively, of the total basin. The residual soils on the ridges are 17.5 percent forested and 4.2 percent nonforested.

Del Moral (1972) has completed a vegetation survey of the watershed. Seven vegetation types were distinguished and their distributions mapped. Most of the area is timbered by relatively homogenous old-growth Pacific silver fir (*Abies amabilis*).

Taber¹ has conducted a preliminary survey of the terrestrial vertebrate activity in the

¹P. R. Olson, J. S. Bockheim, F. C. Ugolini, and others. A terrestrial-lake interface program, Findley Lake watershed. Coniferous Forest Biome Internal Report No. 25. (In press.)

watershed. The elk (*Cervus canadensis*) and pikas (*Ochotona princeps*) have a noticeable impact on the vegetation of the basin. Migratory vertebrates such as deer (*Odocoileus hemionus*), elk, and birds could influence the movement of nutrients in or out of the basin. In addition, the elk activity in some of the meadow areas has obviously disturbed the soil.

Snow accumulations of 4 m often occur in the Findley Lake basin. The open surface period on Findley Lake is approximately 4 months. The lake frequently is not free of snow cover until late July and usually starts to close about mid or late November. A thin layer of ice will often form in early November and soon thereafter, snowfall will cover the surface. The snowfall accumulates rapidly and insulates the surface from additional freezing. The latent heat of the lake water thaws the ice layer originally formed and the snowpack effectively supports itself. As snow accumulates, the light penetration is greatly reduced. In February of 1972 there were 2.9 m (9.5 feet) of snow; the light readings beneath the snowpack were approximately 1.4 lux—0.03 percent of the surface illumination. The oxygen concentration of the water column was close to saturation except within 2 m of the bottom where the oxygen decrease was quite abrupt. Temperatures at this time ranged from 1° C at the surface to 3° C at 25 m.

Limnological surveys were performed by Welch (see footnote 1) on a monthly interval during the open summer period. Findley Lake is extremely clear with visibility extending to depths of 15 m. Since the lake is relatively deep (about 28 m) and unproductive, the hypolimnion during the summer period remained well oxygenated. Maximum water temperature noted at the lake surface during the surveys was 18° C. The dominant zooplankton found was *Diaptomus shoshone* with a modest population of *Holopedium gibberum* present early in the season. The *Diaptomus* population persisted after 3 months of snow cover.

The analysis of water samples by Spyridakis (see footnote 1) is covered more extensively by Taub et al. (1972). Mean values

of the most pertinent variables were: total phosphorus 5 $\mu\text{g}/\ell$, orthophosphorus 1 $\mu\text{g}/\ell$, nitrate-nitrogen 3 $\mu\text{g}/\ell$, silica 76 $\mu\text{g}/\ell$, calcium 1 mg/ ℓ , magnesium 0.6 mg/ ℓ , sodium 1 mg/ ℓ , and potassium 25 $\mu\text{g}/\ell$. Chlorophyll determinations were 0.3 $\mu\text{g}/\ell$ and primary production was 370 mg C/m²/day.

Other surveys which are relatively complete at this time are the paleoecological analysis by Tsukada (see footnote 1) of numerous 1 m long sediment cores. These cores are being analyzed for concentration of pollen, diatoms, *Cladocera*, inorganic elements, and organic chemicals including chlorophyll. The 1 m cores were not sufficiently deep to give a complete record; however, they did disclose the fact that the surrounding environment had been disturbed at least twice in the recent past. There was evidence of a fire with subsequent pollen change and, in a deeper portion, a 500 percent rise in sedimentary chlorophyll. Longer cores will be necessary to explain this phenomenon. Soil profiles disclosed evidence of two relatively recent fires as well as three volcanic ash depositions.

A macrobenthic invertebrate survey was taken by Paulson (see footnote 1) of the lake, the ponds, and the interconnecting streams. May flies and caddis flies appear to be the dominant consumers in the lake. May flies were represented by Baetidae and caddis flies by two species of Limnephilidae. Midge larvae were present, two species of stone fly and also Simuliidae in the creek. In addition a sphaerid clam and a planorbid snail were found in fair abundance. Three species of amphibians were abundant in the lake and pond: rough-skinned newt (*Taricha granulosa*), western toad (*Bufo boreas*), and Cascades frog (*Rana cascadae*). Less common were the northwestern salamander (*Ambystoma gracile*) and the Pacific treefrog (*Hyla regilla*). All evidence to date indicates there are no fish present in the lake.

Present and Future Programs

Year one study on Findley Lake was primarily a survey year. The effort at present is

directed at a continuation of the previous research with a higher resolution to supply the necessary input to modelers. Studies will be intensified on nutrient availability and quantification of primary, secondary, and tertiary production in both the terrestrial and aquatic environments.

The objective of the proposed pedological study by Ugolini is to understand soil-weathering processes and their relations to the biogeochemical cycle. Gravitational water interconnects the atmospheric, biological, lithological, and hydrological components of the biosphere, bringing the reactants together and transporting the end products to new sites. The very essence of soil formation is the migration of ions and particulate matter. Prior to establishing the kinds and rates of migration it is necessary to acquire a knowledge of the soil system in both its chemical and mineralogical composition. Thus estimations of nutrient capital in soils and forest floor of the Findley Basin will be determined.

The common denominator throughout the entire ecosystem is water. Water input as precipitation will be determined and followed through the aerial portion of the system. Thus crown wash and stemflow analyses, both qualitative and quantitative, are essential as well as determination of litterfall rates. The elements of prime concern will be initially N, Ca, Mg, K, and P. This aspect will be investigated by Cole and Gessel who will follow water through the soil system collecting leachates beneath the forest floor, at the boundary between A and B horizons, beneath the rooting zone in the C horizon and within the ground water table. Techniques used here will be similar to those previously reported for the Thompson Site (Cole and Gessel 1968).

The surface water flow within the basin will be surveyed and chemically analyzed by Spyridakis. Many of the surface flows are temporary in nature associated with snow-melt; hence, the quantity of surface flow in the upper system will not be critically determined, but Wooldridge will quantify the hydrologic flow from the entire basin. The nutrient accumulation within the snowpack will also be determined.

Nutrient levels in stream and lake water as a function of seasonal variations and sampling location will be determined by Spyridakis. Determinations will include temperature, conductivity, suspended and dissolved solids, light penetration, turbidity, color, dissolved O_2 , pH, soluble and particulate C, chemical oxygen demand, dissolved SiO_2 , Na, K, Ca, Mg, Fe, Al, Mn, chloride, sulfate, bicarbonate, and carbonate. In addition, the lake sediments will be characterized and their contribution to the overlying waters will be determined.

Welch will determine the annual and seasonal primary production in the lake and relate it to the available nutrients. Special attention will be directed to regulation and control dictated by the elements which may be limiting. Attention will be directed to the phytoplankton cell size and their utilization by zooplankton. The zooplankton composition and biomass will be determined on a regular sampling schedule. The predation impact upon zooplankton will probably be quite minimal, because of the lack of fish in the system; however, observations will be made to determine the potential consumption by insects and amphibians. A consideration for the fourth year of study may be the introduction of cutthroat trout into the lowest pond in the lake basin to determine the impact of predation upon the secondary production, after a comparison of the pond to the lake for a period of time.

The contrast existing between the two ponds and the lake presents an interesting study by itself. Both ponds are 0.4 ha in area but have different depth profiles. The upper pond is only 1.5 m deep and with the loss of the snowpack in midsummer will cease to overflow and decrease to 1.0 m in depth. The lowest pond has not been accurately sounded but appears to be at least 10 m deep and continually receives the overflow from the upper lake. The shallow pond opens earlier in the summer, has a higher heat budget, and freezes earlier in the fall. This contrast will provide an interesting comparison in studies of decomposition, lake bottom water interface, and growth and reproduction of amphibians and invertebrates.

One of the concerns in the aquatic area is

the self-sustaining capabilities within that area and the rapidity of recharge when the system is limited in some important essential. Questions that have been asked repeatedly in the past deal with the role or importance of decomposition in the aquatic system. The Findley Lake basin presents a unique opportunity to measure the dynamics of decomposition when light is abundant and when light is greatly reduced or eliminated for a 6 month period by snow cover. Findley Lake will be used primarily as a comparison to the other three lakes in the system as discussed by Taub et al. (1972). The flux and pool sizes of carbon in the water column will be determined by Lighthart from a compartment analysis of (1) dissolved inorganic carbon, (2) phytoplankton, (3) zooplankton, (4) dissolved organic carbon, (5) detritus, and (6) heterotrophic bacteria using a C^{14} technique. This technique requires the measurement of primary productivity as the initial step in measuring exchanges between compartments. The role of the aerobic, facultative anaerobes, and anaerobic bacteria will be determined by Matches.

The oxidation of organic matter in the water column to be done by Packard will be estimated by means of an oxygen uptake method measuring enzyme activity (Packard 1969). By this method he will compare the seasonal changes in respiratory activity of phytoplankton and zooplankton. Pamatmat will determine the annual deposition of organic matter on the lake basin and its rate of decomposition. This will be determined by placing in the sediment a bell jar equipped with oxygen probe, thermistor probe, and a stirring mechanism (Pamatmat and Banse 1969). The oxygen loss will be monitored with regard to time so that consumption rates may be determined. This will be related to the oxygen budget of the overlying water column.

Estimates of the contribution of detrital biomass to the aquatic food chain will be determined by Taub. This will involve the biomass estimate, and its organic carbon, organic nitrogen, and caloric contribution to zooplankton, benthic invertebrates, and amphibians. In addition, Taub will investigate the biological aspects of nitrogen transforma-

tions (Klucas 1969). An overall nitrogen balance estimate will be determined from estimates of nitrogen fixation and denitrification. Attempts will also be made to determine the transfer from detrital material such as chitin and protein to the dissolved plant nutrient ammonia. The interchange between the various dissolved states of nitrogen, ammonia, nitrate, and nitrite will also be investigated.

Discussion

The Findley Watershed relates to the overall objectives of the Coniferous Biome in three specific ways:

1. It provides an excellent opportunity to study linkage between terrestrial processes and the limnological properties of a lake system. The research is designed to assign values to the rates and quantities of elemental and organic exchange between these systems.
2. Findley Lake represents an extreme in oligotrophic conditions in lake systems and should provide a very interesting general lake model. It will serve as an excellent comparison with the lower three lakes of the Lake Washington drainage basin in studies of nutrient income vs. productivity relationships. Consequently, it is a critical component of the four lake program of the Coniferous Biome.
3. Because of the similarity in terrestrial community structure between Findley Lake and some of the reference stands at the Biome's H. J. Andrews Intensive Site (Gessel 1972), it provides a linkage between the two biome study sites. The effort at the Andrews Site will concentrate on unit watershed models, which will include transpiration, terrestrial primary production, and stream hydrologic models, all of which should have excellent application in the Findley watershed.

To study the interface phenomenon, Findley Lake has been diagrammatically stratified into a series of discrete ecosystem components connected by transfer functions. Figure 2 represents a first approximation of how these components are interconnected

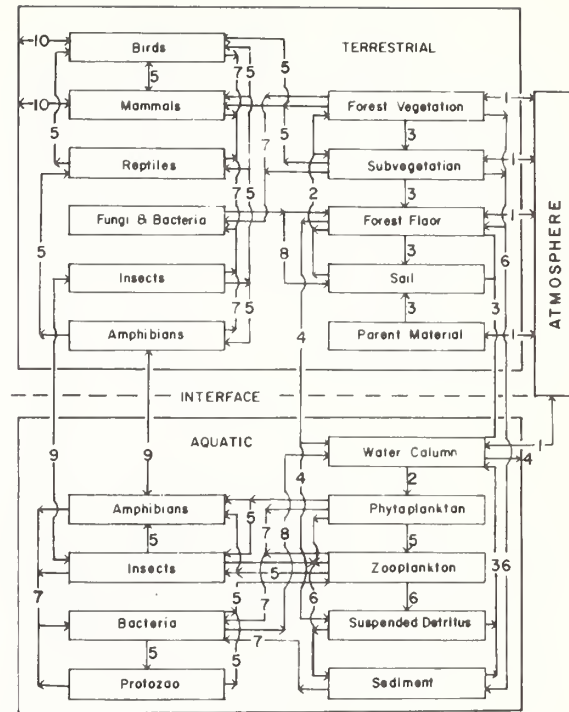


Figure 2. Terrestrial-lake interface diagram with transfer functions numerically listed: (1) atmospheric exchange, heat, light, water and gas; (2) nutrient assimilation; (3) nutrient leaching; (4) hydrological output; (5) consumption; (6) detrital contribution; (7) decomposition; (8) return from decomposition; (9) movement across interface; (10) migration in and out of watershed.

and the nature of the linkage between the terrestrial and aquatic systems. Each of the component boxes will necessitate a quantitative estimate of the biomass or effective reservoir involved. The pathways between components will not only involve a quantitative estimate but also a measure of rate of movement between the components. As the research progresses, the level of resolution will become extremely critical before a total systems analysis is possible. A few important variables which will be kept in mind are: (1) spatial dimensions of the system under study, (2) time base of the study, and (3) the nutrient elements and/or caloric equivalents of the components. It is very likely that the modeling effort will help prescribe a desirable time base.

Acknowledgments

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A comparative study of four lakes ⁶⁰ []

P 21-32
6020

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Abstract

It is increasingly evident from many unfortunate case histories that lake communities are sensitive in a variety of inadequately understood ways to watershed management practices and abuses. If we are to conserve or manage our array of lakes of the Coniferous Biome successfully, we must gain a sufficient understanding to predict the impact of various perturbations on the general lake community structure and production. Initial effort in the Coniferous Biome is being directed toward an intensive comparative study of an array of four lakes in a single watershed that provide a spectrum of human disturbance and manipulation. These are lakes Washington, Sammamish, Chester Morse, and Findley in the Lake Washington-Cedar River Drainage. A study of Cedar River, the main drainage system and a link between two of the lakes, contributes to both the lakes' study and the smaller stream investigations at Andrews Forest.

The Place of Lake Studies in the Biome

It may well be asked why there should be an intensive study of lakes within a CONIFEROUS BIOME. Certainly, the biome is named for the most conspicuous organisms, the terrestrial conifers. However, it can be shown that aquatic studies and the terrestrial studies each have much to gain by being combined.

Unlike the European IBP, the US IBP chose to combine the initial working groups for Freshwater Productivity and Terrestrial Productivity. It was anticipated that this approach would best encourage truly biome-wide studies, not artificially divided by discipline boundaries, such as the Findley Lake study which is discussed in the previous paper. This Biome also includes studies of the marine contribution to freshwater and terrestrial communities by anadromous fish.

Limnologists have long recognized that the terrestrial influences on lakes are of utmost importance. The physical characteristics of a lake are determined largely by its topology and climate which will determine the degree and frequency of mixing. It had long been thought that lakes progressed from oligotrophic to eutrophic as an inevitable sequence. Margalef (1968) and Odum (1969) have suggested that lakes will progress toward increased oligotrophy if the surrounding land does not contribute nutrients. Thus the major successional pattern of a lake may be determined by the terrestrial input.

The nutrient inputs to a lake are very largely determined by the nature of the soil, the land use, and the amounts and patterns of water flow within the drainage basin. Since the major nutrient inputs may be made by the streams, rather than by shore drainage, events quite some distance from the lake can exert major effects. The Biome study provides greater opportunity for evaluating terrestrial

inputs into the lakes. Recent studies have shown this kind of information to be necessary in considering effects of land use.

The terrestrial scientists should not be unmindful of the effect that aquatic bodies exert on the surrounding land mass. Man's needs for water have resulted in virtually all civilizations developing in proximity to river drainage basins. Locally, the impact of water on man's land use is also obvious. Seattle developed into a major city because of its location and port facilities on Puget Sound. Lake Washington has had an impact on Seattle by preventing growth eastward in a contiguous fashion. A great desire for waterfront property has prompted the development of homes and parks all along its shore front, and therefore brought about the necessity of bridges and major road systems to permit residents of the east shore to have convenient access to Seattle. Similarly, the existence of Lake Sammamish and its recreational and esthetic assets have created the development of parks, communities, and therefore, roads, along its shore. Because Chester Morse Lake serves as a water supply for Seattle, the entire watershed of this lake has been fenced off and been inaccessible to the public for 60 years. Land use has been restricted to controlled logging designed so as to protect water quality. Within the Chester Morse watershed, Findley Lake has been protected incidentally.

Aquatic bodies also influence terrestrial communities by the frequency and extent of floods. The temptation to build on level land has resulted in construction on flood plains and the subsequent need for dams and other flood control measures. These in turn have altered the terrestrial environment and the potential uses of the land.

The distribution of terrestrial wildlife is also influenced to a very great extent by the availability of the water supply. A host of water birds collect their food from the water but otherwise nest and conduct the nonfeeding parts of their lives on the land. In addition, there are animals such as otters (*Lutra canadensis*), raccoons (*Procyon lotor*), and bears (*Ursus* spp.), which take a rather substantial amount of their food from aquatic bodies, especially after the salmon spawning.

Over geological timespans, water has a major impact on the land. The streams and rivers are major sculptors of the terrestrial topology. Lakes are not merely a sink for upland nutrients but may become the source of future land. Much of our prime agricultural land is lake fill. The occurrence of peat in the local drainage system gives further evidence that much of our present land was previously occupied by an aquatic community.

Characteristics of the Four Lakes

The four lakes in the Coniferous Forest Biome's Cedar River intensive site—Washington, Sammamish, Chester Morse, and Findley—provide contrasting conditions (fig. 1). The physical parameters of the lakes are shown in table 1.

1. Lake Washington (fig. 2), the lowermost lake, has a documented history of eutrophication and recent sewage diversion. The dominant fish is the anadromous sockeye salmon (*Oncorhynchus nerka*) which was introduced about 30 years ago. Other anadromous and resident fish populations also occur here. The lake is used intensely for recreation, including sports fishing. The shores of the lake are largely urbanized.
2. Lake Sammamish (fig. 3) represents an intermediate condition, as it was oligotrophic until very recently, underwent limited eutrophication as the forest was replaced by an increasing urban community, and is currently undergoing sewage diversion. The response of this lake to sewage diversion has been substantially less dramatic than that of Lake Washington. Surprisingly, the hypolimnion is anerobic much of the summer. Some of the same fish species, including sockeye salmon, occur here as in Lake Washington, but in smaller numbers. This lake drains into Lake Washington from the north via Sammamish Slough.
3. Chester Morse Lake (fig. 4) is the uppermost of the two large lakes in the Cedar River watershed. Although the lake level

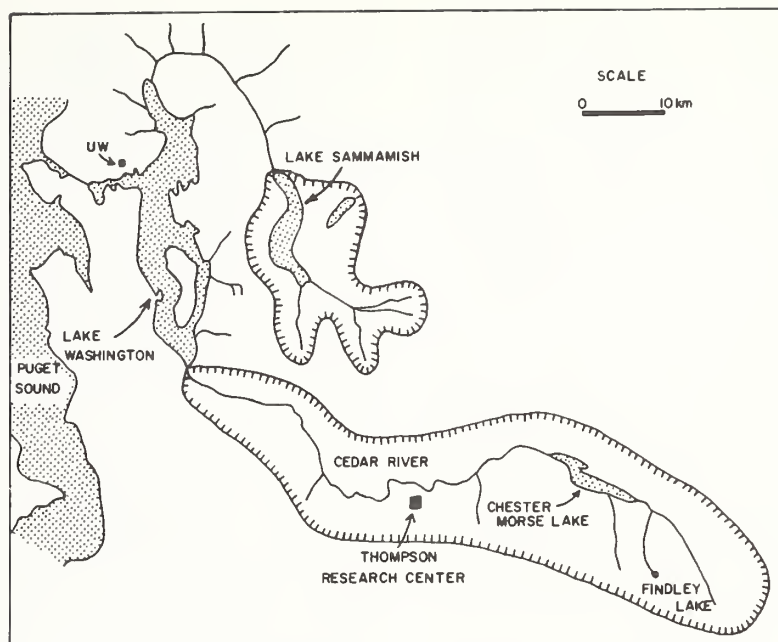


Figure 1. Map of Lake Washington drainage.

Table 1.--Physical characteristics of lakes in Lake Washington drainage basin

Lake	Maximum depth	Mean depth	Area	Volume	Length	Elevation	Water exchange time
	<i>m</i>	<i>m</i>	<i>km²</i>	<i>km³</i>	<i>km</i>	<i>m</i>	<i>years</i>
Findley	30 ¹	10 ¹	0.09	0.0009 ¹	—	1,131	—
Chester Morse	35	13.0	6.54	.085	8.1	473	0.3
Sammamish	31	17.7	19.8	.350	12.9	12	2.2
Washington	64	33.0	87.6	2.884	31.5	8.6	3.0

¹Tentative values.

was slightly raised in 1902, the lake in other respects is the least disturbed major lake in the state. Access to the lake has been rigidly controlled since 1911 and no fish have been planted or harvested since that time. It contains no anadromous fish, but has resident populations of rainbow (*Salmo gairdneri*), Dolly Varden (*Salvelinus malma*), and whitefish (*Prosopium* sp.). The shore is completely undeveloped.

4. Findley Lake (fig. 5) is among several small lakes in a totally unmanipulated watershed. It and its watershed are being used in an integrated terrestrial-aquatic study. The land area consists of undisturbed mature coniferous forest. The lake has no resident fish population but has zooplankton and salamanders in moderate abundance.

Specific tasks of the lake-stream study in the Lake Washington-Cedar River watershed include assessment of (1) terrestrial influences, including forest and urban land use, (2) nutrient budgets, (3) sources of energy to support the food chain, (4) community structure and metabolism, (5) effects of food availability on successive trophic levels, (6) effects of fish on lower trophic levels, (7) effects of anadromous fish on other fish populations, and (8) outputs to the marine community by anadromous fish.

Research Program

In 1971, fieldwork was initiated on chemical budgets, primary and secondary productivity, and fish populations, in coordination with other concurrent studies. A literature compilation of past aquatic studies in the watershed was completed and the transfer of pertinent data to the IBP data bank initiated. A major hydrological study of the lake-river system was initiated by another agency (RIBCO, River Basin Coordinating Committee). Decomposer studies were organized in conjunction with the terrestrial program. A preliminary interface study on Findley Lake watershed was accomplished. A generalized trophic level model was developed and its

shortcomings were analyzed. Modeling efforts on existing data from other lakes were initiated by the modeling group.

In 1972 the fieldwork mentioned above has been expanded and fieldwork on decomposition and nutrient regeneration processes has been initiated. Field effort and modeling structures are reorganized into subsystems of bottom related processes, water column processes, and higher consumer dynamics. Models of optimum strategies and density dependent relationships are being developed. Detailed descriptive models of the lakes will be completed. Data sets at potential extrapolation sites are being identified and a coordination framework was established.

In 1973 the full field program will continue with phasing and evaluation of specific studies, including elimination of those which have either met their objectives or which are not profitable lines of pursuit. Greater emphasis will be placed on using hydrological data and interfacing with terrestrial aspects of the program as well as on perfecting subsystem models and linking them together into a more complete model. Coordination with extrapolation site programs will be increased, including data set analysis.

In 1974, successful and fruitful programs will be continued as necessary, with phasing of research in many instances to accomplish tasks deferred for orderly sequential progression under limited funding. Major efforts will be directed to integration of all work and to use of extrapolation data for model validation and generalization of intensive site results.

Focus of Research Program

The stream-lake study will address a number of questions¹ which have relevance to both science and analysis of environmental impacts. These questions are concerned with: (1) the mechanisms by which purely physical constraints, such as structure of lake basin,

¹These questions and the subsystem models have been developed with the help of the modeling group. Mr. Larry Male of the Center for Quantitative Science, University of Washington, is particularly acknowledged for his contributions to these ideas.

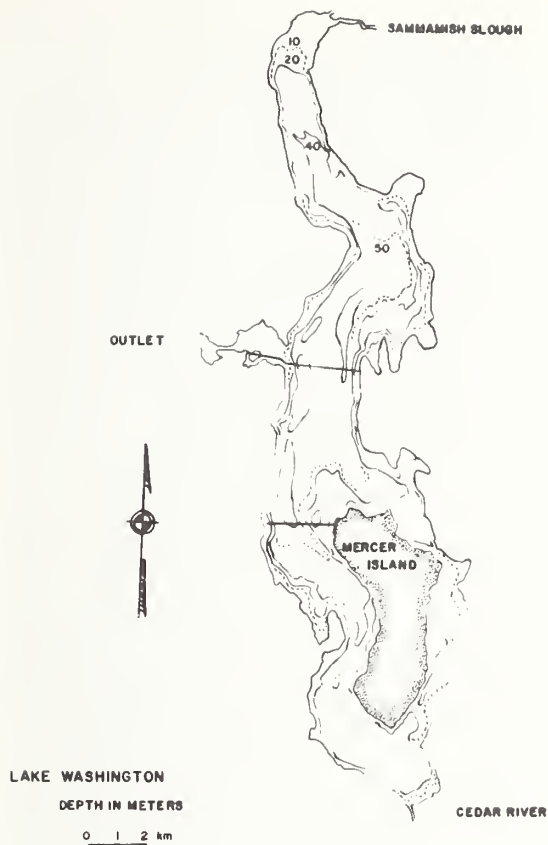


Figure 2. Map of Lake Washington.

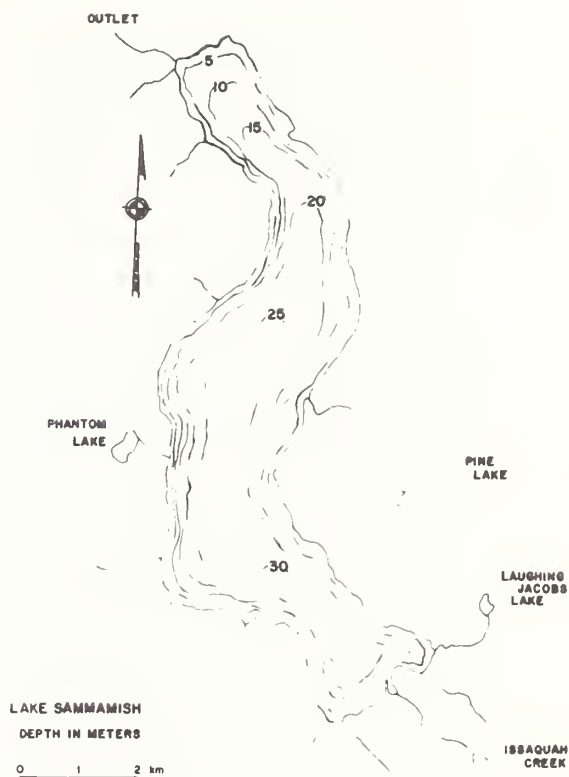


Figure 3. Map of Lake Sammamish.

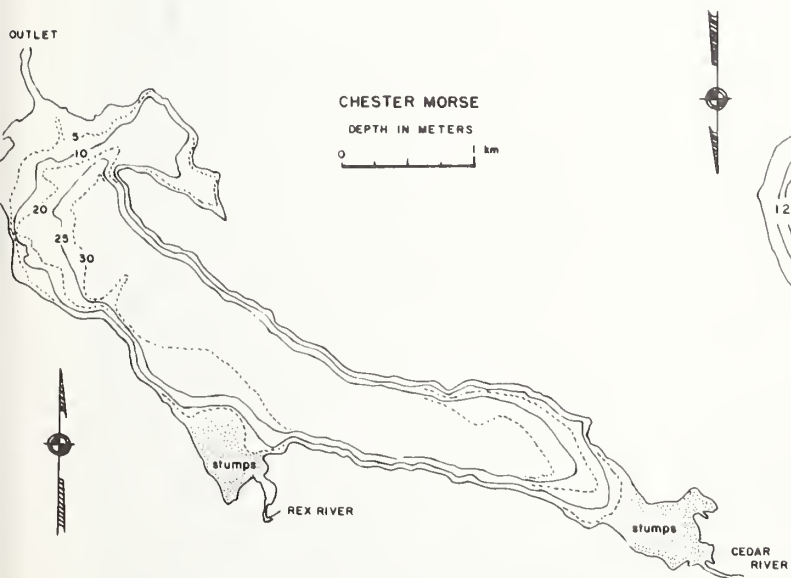


Figure 4. Map of Chester Morse Lake.

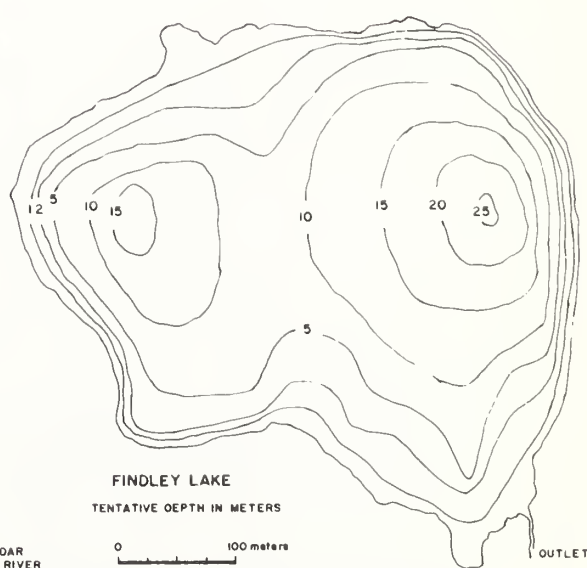


Figure 5. Map of Findley Lake.

climate, surrounding terrestrial environment, prevailing winds, lake circulation dynamics, rates of water and inorganic nutrient inflow and outflow, and chemical precipitation of essential nutrients control the productivity, water quality, and community structure of aquatic ecosystems; (2) the dynamics of nutrient and energy cycling through both biological and physical processes; (3) the mechanisms by which community structure may inhibit or enhance overall productivity and water quality; (4) the response of complex aquatic ecosystems to a variety of natural and artificially created disturbances; and (5) the mechanisms these systems have evolved for coping with these disturbances. The nature of these questions justifies the coordinated program which is planned. Some of the questions this program will bear upon and how they intend to be tackled will now be discussed.

The phytoplankton and bacterial communities in lakes not only provide the basis for complex food webs, they essentially control the overall water quality and the apparent state of eutrophication. The sustained abundance and species composition of the bacterial and phytoplankton communities depend to a large extent upon the rate at which they are supplied with essential inorganic nutrients and energy sources. Most of these compounds are introduced from the surrounding terrestrial environment and the atmosphere through biological fixation processes. The rate at which a lake is supplied with allochthonous materials may determine its productivity structure. Several mechanisms may be responsible for determining a lake's response to allochthonous nutrient input. These mechanisms relate both to the supply of nutrients to the phytoplankton and bacteria communities and to the physical and biological forces which influence the production dynamics of these communities.

1. **Dynamics of release of inorganic nutrients from allochthonous organic material of varying nutrient richness:** The first indication is that nutrients in nutrient poor organic material, e.g., wood, are released slowly. Since the four lakes in this study can be characterized by the nature

and extent of allochthonous input, this mechanism can be studied.

2. **Nutrient availability as a function of thermal distribution, circulation dynamics, and cycling dynamics of other chemical compounds:** Vertical density gradients (determined by vertical thermal distribution gradients) can control the availability of essential nutrients to autotrophic organisms. The density gradients function as a barrier to the mixing of nutrients from deeper waters into the productive surface waters. Since the density barrier also inhibits the passage of oxygen from the surface into the deeper waters the deeper waters sometimes become depleted of oxygen. This anerobic condition enhances the solubility of compounds which bind phosphorus in forms unavailable to phytoplankton. Thus, the deep waters may be rich in nutrients which are relatively unavailable to autotrophic organisms. The four lakes in this study vary greatly in the formation of their density gradients and thus their capacity to trap nutrients. This theory is only partially applicable to any particular lake since there exist other mechanisms for distributing nutrients. The shape of the lake basin, direction and strength of prevailing winds, internal circulation currents, disturbance of the bottom sediments by mechanical mixing, and dynamics of nutrient transport through the reduced layer of the sediment are all mechanisms which are being studied to bear upon the problem of nutrient cycling.
3. **Biological cycling of nutrients:** Since the communities of phytoplankton and bacteria in lakes are often limited by the availability of essential nutrients they have tended to evolve elaborate mechanisms for the conservation and recycling of nutrients. In the absence of these mechanisms, production would most likely be nil. Nutrients cycle through communities of phytoplankton, zooplankton, bacteria, protozoans, and littoral aquatic plants. The nature of these cycles and how they operate with-

in the restrictions of the physical environment are being tackled. Since the four lakes in this study have evolved to their present structure in the presence of different nutrient stresses we might expect them to exhibit various capacities to conserve and cycle nutrients.

4. **Effect of community structure on productivity and distribution of energy:** The production of herbivores (zooplankton) cannot be explained entirely by production of primary producers (phytoplankton). The physical form of the production (i.e., size distribution or colonial form of algal cells) may preclude consumption by zooplankton. However, zooplankton may in fact contribute to changes in the physical form of primary production by being size-selective feeders. Since changes in the form and species composition of phytoplankton communities are indices of pollution and eutrophying environments this process is being investigated.

In the same way that changes in the physical form of phytoplankton production may control the production of zooplankton, the community structure, size distribution, and spatial distribution of zooplankton control the feeding behavior and subsequent production of predators.

The terminal link in the food web of three of the study lakes is the community of fish species. Much literature has been devoted to models which try to explain the population dynamics of these organisms without incorporating their interaction with the environment. The communities of fish can influence the nature of production by altering the community structure of other vertebrate and invertebrate communities upon which they feed and indeed may alter the entire community (Hurlbert et al. 1972). Their own production dynamics are related to the structure and abundance of the prey communities and also to mortality dynamics which are determined by the state of the physical environment at critical life stages. Three projects will bear upon the questions related to the fish community.

Presently, a three submodel system (figs. 6 and 7) is being used to develop the proposed field studies; these are organized around water column, bottom related, and higher consumer processes. These subsystems were chosen because the couplings within each are more tightly linked and the span-of-time resolutions

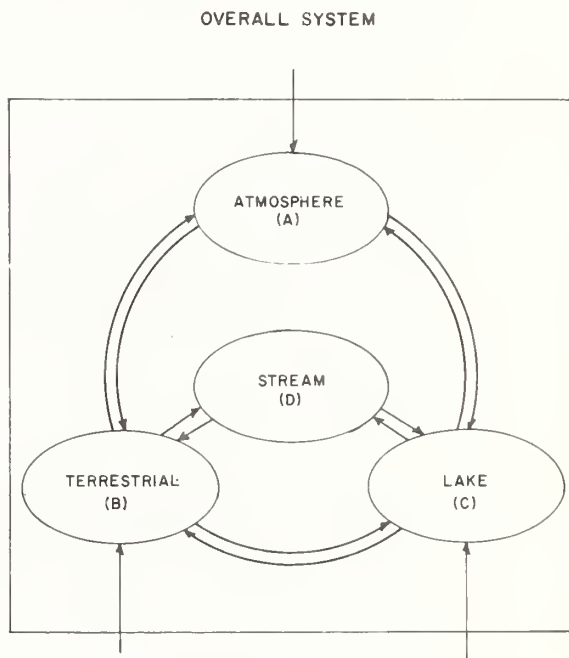


Figure 6. Overall system categories.

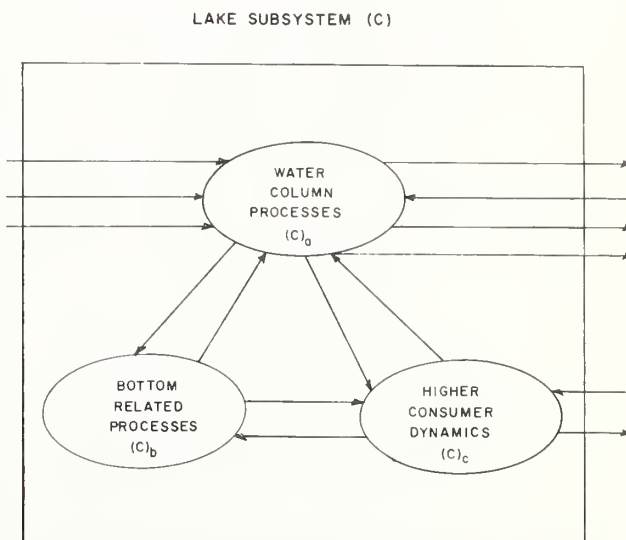


Figure 7. Lake subsystem categories.

more similar than between the different sub-systems. For example, the processes in the water column involving exchanges between nutrients, algae, shortlived zooplankton, and bacteria can better be handled by a single team than by several teams, each interested in a specific trophic level. Further, this information may have to be handled on a daily or hourly basis, whereas the higher consumer production, e.g., fish, will be handled on a seasonal basis.

Studies Planned for 1973-74

The individual studies tentatively planned for 1973 and 1974 for the four lakes are shown in table 2. These are described briefly here. The interface study specific to the Findley Lake watershed is described in the previous paper.

Water Column Process Studies

The categories and relationships are shown in figure 8. Much of the past work in the Cedar River drainage lakes defined the annual nutrient supply to Lake Sammamish and

documented its rate of recovery compared to that of Lake Washington as a result of nutrient diversion. Recently, limnological conditions have been monitored in Chester Morse and Findley Lakes to compare their trophic character with that of Lakes Sammamish and Washington. Ultimate objective is to develop a model with enough generality to encompass the range in trophic character now observable among the lakes.

Lake Washington responded rapidly to a diversion of over one-half its annual supply of phosphorous. Edmondson (1970) has documented its recovery to a trophic state similar to that recorded over 20 years ago in a matter of only 3 years after the completion and 7 years after the beginning of sewage diversion. Lake Sammamish, a mesotrophic lake with similar flushing time, located only 10 miles to the east of Lake Washington, has not responded noticeably in 3 years following nutrient diversion. Possible reasons for this difference in rate of response involve the morphometry of the two lakes.

The nutrient input to the lake and the levels of dissolved inorganic nutrients will be related to the growth and production of phytoplankton and its consumption by zooplankton. These studies will be in sufficient detail to examine changes in species composition and the importance of size categories as they may relate to optimum feeding strategies. More detailed, but less frequent estimates of the flow of carbon through all components of the food web will be made by the techniques of Saunders (1969) using radioactive bicarbonate, radioactive detritus, and radioactive dissolved organics. Both of these field-oriented studies will be correlated with the modeling on the dynamics of nutrient distribution and flow through aquatic ecosystems. A deferred study concerns the role of fungal parasites on algae to explore the hypothesis that algal blooms may cease through disease processes, rather than through the limitation of nutrients.

The mathematical models which have been developed to explain the production dynamics of phytoplankton production admit that the concentration of phytoplankton may vary continuously from the surface to the lake bottom.

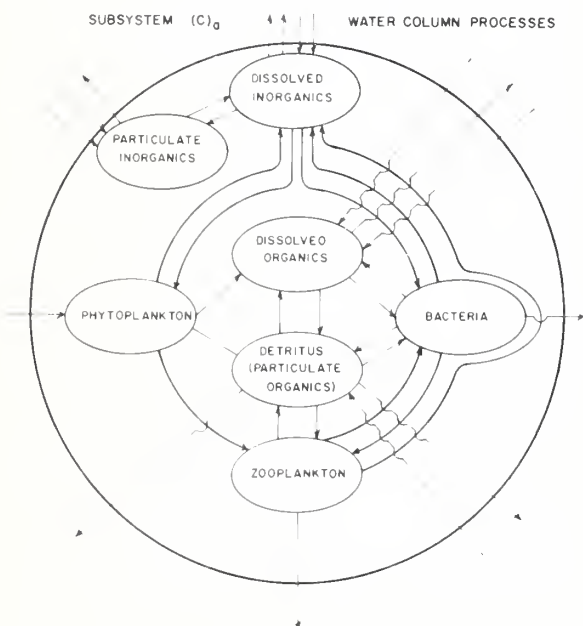


Figure 8. Categories and relationships of sub-system (C)_a; water column processes.

Table 2.--Proposed lake studies (by investigator and abbreviated title)

Aquatic Director: R. L. Burgner
 Lake Studies: F. B. Taub, Chairman

	Department	University	Study
Water Column (E. B. Welch, Chairman)			
1. E. B. Welch	Civil Engineering	Univ. Washington	Zooplankton-production
P. R. Olson	Forest Resources	Univ. Washington	
2. E. B. Welch	Civil Engineering	Univ. Washington	Phytoplankton-production
3. B. Lighthart	Inst. Freshwater Studies	Western Washington	Carbon web
4. B. Lighthart	Inst. Freshwater Studies	Western Washington	Bacteria
5. T. Packard	Oceanography	Univ. Washington	Oxidation-respiration
6. F. B. Taub	Fisheries	Univ. Washington	Nitrogen transformation
J. T. Staley	Microbiology	Univ. Washington	
7.*D. E. Spyridakis	Civil Engineering	Univ. Washington	Nutrient budgets
R. F. Christman	Civil Engineering	Univ. Washington	
Bottom-Related Processes (D. E. Spyridakis, Chairman)			
8. D. E. Spyridakis	Civil Engineering	Univ. Washington	Nutrient budgets
R. F. Christman	Civil Engineering	Univ. Washington	
9. F. B. Taub	Fisheries	Univ. Washington	Detrital input
10. J. R. Matches	Fisheries	Univ. Washington	Bacterial decomposition
11. M. M. Pamatmat	Oceanography	Univ. Washington	Oxidation
Higher Consumers (R. R. Whitney, Chairman)			
12. R. L. Burgner	Fisheries	Univ. Washington	Limnetic fish
R. E. Thorne	Fisheries	Univ. Washington	
13. A. C. DeLacy	Fisheries	Univ. Washington	Limnetic fish feed
14. R. S. Wydoski	Fisheries	Univ. Washington	Benthic-littoral fish
R. R. Whitney	Fisheries	Univ. Washington	

*See also Bottom-Related Processes.

The net rate of primary production at any particular depth depends upon the temperature, light intensity, essential nutrient concentration, and zooplankton grazing pressure at that depth. The vertical distribution and abundance of phytoplankton is thus a function of varying net production, sinking rates of algae and mixing dynamics of the water column. The total production per unit area of lake surface may be obtained by integrating the concentration of phytoplankton from top to bottom. The next step is to incorporate the size selective feeding of zooplankton and determine its effect upon production (since algal cells of different sizes possess varying capacities to absorb nutrients).

The effective grazing rate by zooplankton is modeled as a function of the phytoplankton density (at high densities the zooplanktons feeding structures become saturated). The efficiency of assimilation of phytoplankton by zooplankton is also allowed to depend upon algae abundance (efficiency decreases with increasing abundance).

The overall model relating the phytoplankton, zooplankton, and nutrients is a system of partial differential equations (in time and depth).

The submodel describing the physical cycling of nutrients (developed in the bottom related processes group) is an integral part of the phytoplankton, zooplankton submodels.

The number and kinds of heterotrophic bacteria will be assessed to give some information on the constancy of community structure of the decomposers. The utilization and ultimate destruction of fixed organic material for the entire system will be estimated by respiration studies and verified by substrate disappearance. The respiration and heterotroph abundance values will also be correlated with the regeneration of nutrients. The nutrient budget and effective concentrations will be assessed. All of the above studies will be carried out in units of biomass or will be convertible to biomass and units of carbon by calculation of size distribution. Determinations of the magnitude of nitrogen transformation within each of the above compartments, as well as the search for evidence nitrogen fixation and its opposite process, denitri-

fication, will be made.

The detailed carbon cycle through the phytoplankton, zooplankton, bacteria and pools of dissolved inorganic carbon, dissolved organic carbon, and detritus are being modeled initially with a varying rate compartment system. The rates of flow between the compartments are to be functions of light, temperature, and PO_4 and NO_3 concentrations. Later the rates will also be modeled as functions of O_2 and S_i concentration. This model will allow an analysis of what paths of the cycling process limit the rate of production.

Bottom Related Process Studies

The compartments are shown in figure 9. The necessary chemical analyses to assess this aspect of the nutrient budget will also be done. Inputs of detrital materials to the sediments and their potential incorporation into higher food chains via bottom invertebrates to the fish will be assessed. The oxidation of organic material will be assessed by respiration rates of the sediments. The disappearance of substrates such as cellulose and chitin and information on the bacteria associated with

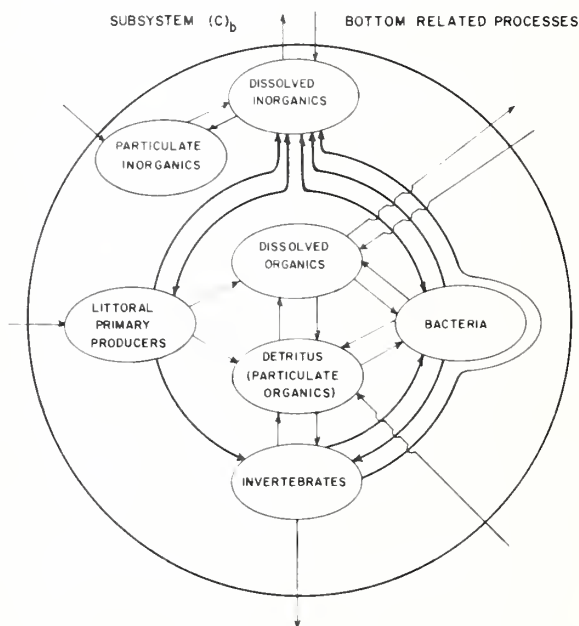


Figure 9. Categories and relationships of sub-system (C)_b; bottom related processes.

these processes will be measured and correlated with nutrient regeneration and respiration rates. The production of littoral materials will be assessed and compared with limnetic production and terrestrial inputs. The combined information on limnetic, benthic, and littoral photosynthesis and respiration will permit comparisons of P/R ratios for the various lakes within this study as well as for wider comparisons.

A sophisticated theoretical model describing the complex physical and biological cycles of inorganic nutrients has been proposed. This model incorporates the features of density gradients as a barrier to mixing, circulation currents, chemical precipitation of essential nutrients, transport and release of nutrients from the bottom sediments as a function of O_2 concentration, pH, and bacterial decomposition, nutrient input in organic and inorganic form from allochthonous sources, and atmospheric input through biological fixation processes. This theoretical model will be made more precise and useful by formulating it as a collection of well-defined assumptions and mathematical equations. This model will allow an analytic comparison of the cycling processes in the four lakes.

Higher Consumer Process Studies

Compartments are shown in figure 10. The measurements of population parameters of young sockeye and other limnetic feeding fish will provide comparative data on seasonal changes in numbers, biomass, growth, and mortality rates relative to possible controlling factors, including recruitment, physical and chemical environment, food availability and characteristics, behavior and competition, predation and other removal. Characteristics, habits, and interactions of the benthic and littoral fish will be studied. Study of the benthic food supply will be temporarily deferred. The interaction between the benthic and littoral fish and the limnetic feeding fish is receiving emphasis. In all cases, there will be a search for understanding of feeding strategies and growth dynamics as they influence community structure of the zooplankton and fish.

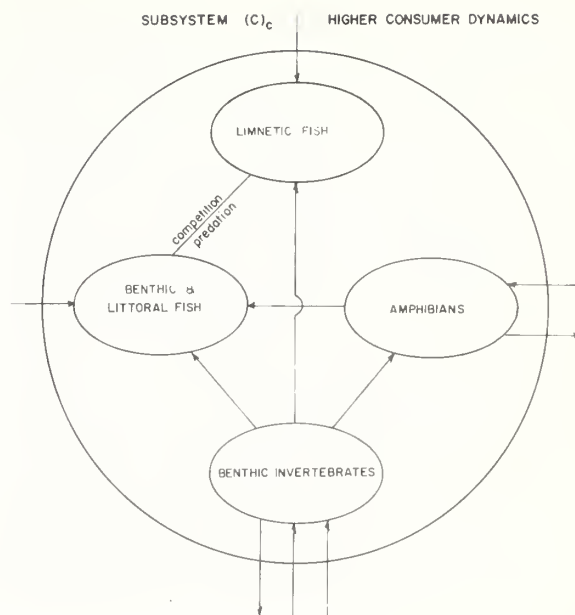


Figure 10. Categories and relationships of sub-system (C)_c; higher consumer dynamics.

The vast food webs, typical of lake ecosystems, seem to be so complicated as to defy description. The higher consumers not only respond physiologically to their surrounding physical environment, they exhibit complex behavioral mechanisms to cope with changing food supplies and varying physical conditions. A conceivable model for this system is a varying rate compartmental model where the rates of transfer among various species depend on the physical environment. Another approach which is finding favor among theoretical ecologists is the theory of optimal strategies. The essences of this theory is that selective processes and adaptive mechanisms tend to produce populations of organisms which strive to maximize their energy intake subject to the physical restrictions imposed by the environment and their own physiological and morphological limitations. If the community structure of the prey organisms available to a predator is known then a mathematical representation of an optimal strategy model will predict the amounts and kinds of prey a predator will ingest. Coupled with models which describe the mortality structure of populations the optimal strategy model will effectively handle the questions concerning

community structure and energy flow dynamics.

It is obvious the subsystems above are artificial and that coordination of techniques and measurements is necessary. For example, the nutrient budget of the lake cannot be developed without the water column and the bottom processes information, nor without the hydrological studies being coordinated with RIBCO and assessment of nutrient sources.

The present (1972) studies are necessarily descriptive, to supply the material for the first rough models. As the inadequacies of the crude models become apparent during the course of 1972, there will be increasing interplay between the modeling and the field investigations and programs correspondingly modified.

Acknowledgments

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The modeling process relating to questions about coniferous lake ecosystems

P.33-36
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Ref-

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Abstract

The role of sound conceptualization and meaningful questions in the modeling process is discussed. The salient features of lake communities are reviewed. Included are factors which must be considered in answering questions involving the higher consumers of lake ecosystems.

Before attempting an analytical model one must conceptualize the system being modeled. If one's conceptualization is good, then one is able to ask relevant and meaningful questions. Since ecosystems are infinitely complex, one must make assumptions and simplifications in constructing analytical models which are within our capabilities. Because of these assumptions and simplifications it is impossible to construct general ecological models—a general model being one which will answer or anticipate all questions. Therefore models must be constructed relevant to specific questions.

A set of meaningful questions should be the foremost component in the strategy which a worker adopts in the construction of a model. These questions allow the modeler to make sets of assumptions and simplifications which make a model both meaningful and workable.

Considering a coniferous lake ecosystem, if one is interested in questions of seasonal succession of phytoplankton or perhaps, more long-term successional changes along a gradient lake nutrient level, then one must construct models which differentiate the algae with respect to species. This model must incorporate algal adaptive mechanisms to critical resources. On the other hand, if the question is one of primary production, then it may be worthwhile

to construct models where the algae are lumped together into a uniform mass of quasi-organisms. This is a fundamental assumption of the Riley et al. (1949) model. But without species differentiation a means of handling the interesting questions in ecology of competition, predation, selection, and adaption is destroyed.

The following are some of the factors we have considered in developing our conceptual framework of a coniferous lake ecosystem. The structure and dynamics of the salient features of aquatic communities are reviewed. Attention is given to processes which have traditionally been neglected in quantitative models.

Generation times in the algae are short. Thus the selection process may be rapid. This can give rise to rapid shifts in the species composition of phytoplankton as the environment changes (Hutchinson 1967). Because of seasonal, diurnal, temporal and other spatial patterns of environmental change, selection processes are in a continual state of flux. The patchiness in spatial distribution of the organisms plus interruption in selection processes by continually changing environmental conditions, allows many species to coexist in the lake ecosystem. The state of being the

best adapted organism vacillates between species with time as the environment changes.

The level of nutrients in a lake ultimately determines the level of phytoplankton which the lake can support. Nutrients are utilized by plants as components of structural molecules, such as DNA, RNA and enzymes. If nutrient levels are in excess of structural demands and other conditions are favorable for photosynthesis, then reproduction can occur. Nutrients are rare elements in lake ecosystems, very eutrophicated lakes being exceptions. Aquatic communities have evolved many mechanisms for their conservation (Pomeroy 1970). Algae and littoral plants can absorb nutrients almost instantaneously from the water. Aquatic plants can take up nutrients as they are available and store them until conditions become more suitable for growth when the nutrients are utilized. Light and temperature conditions necessary for photosynthesis are much more predictable, with definite seasonal and diurnal patterns, than nutrient levels, which the algae cells encounter more or less randomly. Then, from the viewpoint of algae, a good strategy to evolve would be a means of acquiring nutrients whenever they occur and waiting to make use of them until sufficient light and temperature conditions (these are predictable) prevail.

In addition to being able to utilize nutrients as they occur, the phytoplankton-zooplankton community recycles nutrients rapidly. As the algae die and sink to the bottom, nutrients are released in two ways. Autolytical release occurs by simple diffusion. Mechanical release occurs when the cell membrane ruptures. Between 25 and 70 percent of the nutrients contained in a sinking, dead organism are released in these ways (Johannes 1968).

Zooplankton eat substantial proportions of the algae. Herbivores are large in relationship to their food supply. Since zooplankton are eating a rich source of essential nutrients, they consume many more nutrients than they need for structural components. The excess is simply excreted into the water.

The classical role of bacteria, as the principal agents of nutrient regeneration is questioned by Johannes (1968) and Pomeroy (1970). Bacteria accumulate nutrients over the level required in growth, as algae do.

Johannes (1968) believes that protozoa, often neglected as important organisms in lake systems, are responsible for regenerating nutrients by eating bacteria and excreting the excess nutrients.

In addition to biological means of nutrient cycling, many purely physical processes affect nutrient distribution in lake systems. Nutrients enter the lake through the inflow (both surface flow and seepage) and precipitation. Nutrients leave the lake through outflow (both surface flow and seepage). Sediments are very important in the nutrient budgets of lakes. They may act as a trap for essential nutrients, such as phosphorous. The phosphorous is tied up by iron and precipitated out at high redox potentials. Decreasing redox potential usually accompanies decreasing oxygen concentration. When the redox potential falls below a certain level the phosphorous goes into solution, thereby becoming available to photosynthesizers in the waters above. In oligotrophic lakes the redox potential is always high and phosphorous bound in falling detritus is lost to the system when it reaches the sediments. The cycling of nitrogen is more complicated and even more intimately tied in with the redox potential. The rate at which essential nutrients are recycled through the community, interchanged with the sediments, and lost and replenished through inflow and outflow determines the productivity of the lake. The response of this system to perturbation, measured not only by the level of productivity but by changes in community structure, is the central theme of our research effort.

Production is usually defined as the total elaboration of organic matter by photosynthetic organisms in a specified time period, while productivity is the production per unit time. Photosynthetic rate depends principally upon light intensity, temperature, and essential nutrient concentration (Riley 1946, Rhyther 1956, Talling 1961). Photosynthetic rate is different for different species of algae (Talling 1955). The production under a unit area of lake surface is the sum over species of the integral with respect to time and depth of the algae densities times their respective photosynthetic rates. The above generalization may appear overly simple; however, the

complexity of lake productivity will become apparent.

The exponential decay of light intensity is a function of depth. Temperature varies with depth. Although factors leading to lake stratification are well understood, the construction of predictive models for temperature distributions in lakes has only recently begun. Light intensity varies with time, because of seasonal and diurnal patterns plus changing weather conditions. There are vertical currents due to advection and eddy diffusion in lakes (Riley et al. 1949). These currents cause temperature, nutrient concentrations, and the population densities to vary with time. We must also consider feedback mechanisms such as self-shading (Talling 1960), and local depletion of nutrients by algae.

Another interesting feedback mechanism involves the relation between phytoplankton and zooplankton densities. The rate of grazing on phytoplankton is determined by zooplankton density and its relative grazing rate (Riley 1947). On the other hand, the relative grazing rate of zooplankton is a function of phytoplankton density; a saturated grazing rate is reached at high algal population densities (Holling 1959, Riley 1947). Zooplankton also influence nutrient availability by excreting soluble nutrients into the water.

In addition to the limnetic plankton communities, there are, in lake ecosystems, littoral communities and, in areas deeper than maximal light penetration, benthic communities. The processes that occur in these communities are somewhat different than in the limnetic community. Littoral communities are similar to terrestrial communities in many respects. Emergent and floating forms have access to atmospheric carbon dioxide. Attached forms have direct access to nutrients held in the sediments; whereas, limnetic algae are free floating and must depend upon large ratios of surface area to volume and upon passive sinking for efficient nutrient absorption. In littoral areas, herbivores are small, relative to plant size. They consume little of the plant biomass. Littoral plants show seasonal die back, with much material being decomposed. As in terrestrial systems, bacteria and detritus feeders are the primary agents of

nutrient regeneration.

Hutchinson and Bowen (1950), in a radio-phosphorous study, showed that littoral plants can soak up and hold a large quantity of nutrients. Thus limnetic and littoral plants do compete for nutrients. The littoral plants are less efficient than algae in absorbing nutrients because of their smaller ratio of surface area to volume. The littoral system's ability to hold nutrients (because of slow nutrient regeneration by bacterial decomposition and relatively small grazing pressure) offsets inefficient nutrient absorption. Phytoplankton, because of their short life span and high predation rate, cannot hold nutrients as long as littoral plants, but they are very efficient in absorbing nutrients.

Deep benthic communities are made up of detritus feeders that feed upon seston raining down from the productive epilimnion. They may be important in nutrient regeneration (Johannes 1968). These animals constitute important food sources for higher order consumers.

A promising theory which may be of great help in generating and answering questions about higher consumers, is that of feeding strategies. For a review of a substantial literature on the subject, see Schoener (1971). The essence of the theory of feeding strategies is that selective processes tend to produce populations of organisms which strive to maximize their energy (essential nutriment) intake. Predators may accomplish this end in several ways; however, it appears reasonable that it would pay to eat the largest prey or the easiest to capture whenever they are encountered, chasing relatively small difficult-to-catch prey only as a last resort. It is currently being demonstrated that this theory applies to a large variety of animals. The consequence is that one is able not only to predict the food habits of individual species but also to estimate their growth dynamics.

Acknowledgments

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U.S. Analysis of Ecosystems, International Biological Program. This is Contribution No. 22 to the Coniferous Forest Biome, IBP.

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Toward a general model structure for a forest ecosystem [p. 45]

P. 37-47
3505

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A primary objective of the Coniferous Forest Biome is the development of a family of models for a forest ecosystem as a whole. This paper will discuss the general structures and forms which represented our views toward the end of 1971. It is emphasized that these are evolutionary; at least part of the value of this paper is as a record of the path we took in model development. The value of these structures in furthering ecosystem theory is also argued.

Thus, a primary focus of this paper is with respect to ecosystem research at the "total system" level, that is, concerning the ecosystem as an object. It is another goal of ecosystem research to study the relations among component parts and further to study the system properties of those parts. Populations, communities, assemblages, food chains, productivity processes, and many other subsystem structures are of interest, in their own right, as are the functional and relational aspects of these structures. In fact, one of the great difficulties in modeling the ecosystem as a (single) object is the strong tendency to perceive the ecosystem as an assemblage of poorly defined subsystems such that the couplings are vague, at best, and often entirely undefined. Model structures are developed which, it is hoped, will contribute to elaboration of these subsystem concepts, as well as the concept of the total system as

object.

A brief statement of my view of models, and of their role in science seems desirable. Any particular model for a real world system (or object) can be decomposed into a set of statements regarding that object. Some of these statements will be definitive, some will represent firm knowledge about the object, and some will be in the form of infirm knowledge or simplifications (which statements we usually call assumptions). If we consider the collection of all possible models for an object, then the set of all statements of definition and all statements of firm knowledge represent all that is known about the object, so that at this level the model, the canonical model, is identical to the state of knowledge about the object.

Working models usually emphasize some elements of knowledge and neglect others, so that in practice the models we use are something less than "complete." However, most working models represent, in a very real way, the knowledge and theory of a real world system. Some subset of the total knowledge is coupled with some set of simplifying assumptions and the collection given a form and structure by a mathematical or relational algorithm or convention. The process puts the present knowledge into a new form. If the new form serves to increase the understanding of the system, then the modeling operation is

successful.

Thus we can see modeling as the imposition of structure on existing knowledge. As such, it is a joint activity between those familiar with forms and structures and those familiar with a body of knowledge. In time, the structure imposed becomes integrated into the scientific paradigm of the object, providing new insight and a base for extending concepts. In this view, modeling is an integral part of the theoretical advance of a subject science, not an external, nor peripheral, activity engaged in by mathematicians or other specialists.

Now I don't think that I am the only one with this view, but there are sufficiently many opposing views among modelers and sufficiently many misconceptions among subject specialists that verbalization of this perspective is essential in an introduction of the present topic. I view our efforts to develop a total ecosystem model as a contribution to the scientific paradigm of ecosystems. Our primary activity as modelers is the conceptualization of theoretical ecosystem structures and behavior. The present paper deals with the structural aspects of a developing family of models for the forest ecosystem at a date late in 1971, and with the strategy we have adopted to pursue our objectives.

Approaches to System Theory and Definition

Klir (1969, 1972) discusses in some detail a variety of definition forms and approaches to developing a general theory of systems. This seems a productive direction and the following section is my own interpretation and elaboration of these passages in Klir. There may be inadvertent deviations from Klir's intent.

The State Variable (or State Space) approach seems to describe the model structure currently most popular in several fields, including ecology. The essence of this approach is that the system is defined as a set of variables, the state variables, and a set of variables representing the environment, in a particular

temporal resolution. A popular version defines compartments, with the state variables describing the contents of the compartments. The definition is completed by specification of algorithms for change of the state variables in time.

Klir has proposed a general systems theory which, although not distinct from the state variable approach, has certain features which apply nicely to study of ecosystems. Specifically, he identifies five ways in which a system may be defined:

1. By the set of external quantities and the resolution level
2. By the given activity
3. By the permanent behavior
4. By the Universe-Coupling structure
5. By the State-Transition structure

The models of the system follow definition forms 3, 4 and 5. Definition form 1 is used in the planning stages of a modeling or data collection activity, and a collection of data is a realization of definition form 2. It follows that definition form 1 is implied by form 2 and by forms 3, 4, and 5. When applied to the same system, the forms must be mutually consistent. In the Coniferous Biome, we have adopted a particular combination of the three model forms for our model of the forest ecosystem. We view each system (or subsystem) as modeled at two levels:

1. Holistically, according to its Behavior (or State-Transition structure).
2. Mechanistically, according to its Universe-Coupling structure.

That is, we view Klir's *Behavior* and *S-T structure* as useful forms for characterizing the holistic behavior of a system "as an object," and consider that such holistic characterization is necessary for each defined system or subsystem. Further, we consider that in most cases we will also wish to model the system according to the *U-C Structure*, that is, as a collection of subsystems, each modeled according to its *Behavior* and with the collection coupled in a manner appropriate to the behavioral forms used.

Some further elaboration of these terms seems necessary, but a formal definition (as in Klir 1969 and Orchard 1972) is inappropriate. An attempt to informally define some of the

terms follows. The external quantities (or variables¹) are those relevant quantities associated with the attributes of the object. Part of them are inputs (produced by the environment) and part are outputs (produced by the object). Specification of these quantities constitutes definition form 1. By definition form 2, an activity is a particular set of values representing the system over a particular set of time instants.

The permanent behavior is a time invariant relation between the outputs of interest and other quantities. In order to develop this in general, it is necessary to augment the specified external quantities by past values of the external quantities (i.e., by a memory), the augmented set of quantities constituting the *principal quantities*. The outputs of interest are then the dependent quantities (a subset of the principal quantities), and the relation is defined between these and the rest of the principal quantities.

It is necessary to emphasize that this definition specifies that the principal quantities are generated from the external quantities alone. If internal quantities (i.e., quantities defined on the subsystems but not on the whole) were allowed, then the state variable approach would be a special case of definition form 3. As it is, the two approaches (S-V and Behavior) have special cases in common.

The State-Transition Structure is defined by recognition of the State as the instantaneous value of the external quantities, of the stimulus as the instantaneous value of the input quantities and by a time invariant relation which sends the system from a particular state and stimulus at time t into the set of possible states at time $t + h$. The S-T structure is a useful special case of the permanent behavior, and in subsequent treatment will not be explicitly identified.

One last point regarding behavior. In either form (of behavior) the time invariant relation can be either deterministic (i.e., the relation is a mapping) or probabilistic (i.e., the relation is one to many) and in the latter case either definition (Behavior or S-T structure) must be

augmented by an appropriate probability function.

Our notation, then, for the holistic definition of the system will be:

$$S = \{Z, M, Y; R\} \quad (1)$$

where Z represents instantaneous input quantities (variables)

Y represents instantaneous output quantities

M represents memory quantities (past values of Z or Y quantities)

and R is the appropriate time invariant relation between Y , on the one hand and Z and M on the other.

It is the specification of the relation, R , which is the goal of ecosystem research at this level. R is the time invariant relation which permits description of the behavior of the system (definition form 3) in place of the simple "data record" provided by definition form 2. In fact, it is a fair statement that a field data collection relates to system definition by the second form and that it is the role of data analysis and theoretical synthesis to progress to forms 3 and 4.

The behavioral representation of the system S as an object, as by (1), is followed by its perception as a coupled collection of subsystems (sub-objects)

$$S = \{S_0, S_1, \dots, S_k; C\} \quad (2)$$

where C is the specification of the couplings among the subsystems S_1, \dots, S_k . Typically, the coupling between two subsystems, say S_i and S_j will be the coupling variables defined by $Z_i \cap Y_j$ and $Z_j \cap Y_i$. That is, some of the outputs of subsystem S_j become inputs of subsystem S_i and vice versa, and these coupling variables define the couplings among the subsystems.

In Klir's theory, it seems to be assumed that all of the external quantities of the system S appear explicitly as external quantities of the subsystems (along with many new quantities which are external to S_i , $i=1, \dots, k$, but internal to S). However, it appears to me that it is the nature of different levels of organization that the external quantities differ not only in resolution and detail but possibly also qualitatively and that definition

¹The quantities are defined on the object. Variables are model counterparts.

of the external quantities of S would be impossible in the context of isolated subsystems.

What is needed is some translation of subsystem external variables into system external variables. Clymer and Bledsoe (1970) have addressed a similar question in consideration of "interfacing" two subsystems at the same level and use the term "slave model" to designate the set of equations for changing resolution. This term seems inappropriate in the context of composition of subsystem properties into properties of the whole; such a process is more master than slave. I have chosen the term "Ghost System"² and notationally designated S_O as the integrating subsystem which derives the properties of the whole from the properties of the parts. In its simplest form, S_O is a resolution expander of inputs and reducer of outputs. Whether it will need to assume a more complex form is yet to be seen.

In this manner we have, by statements (1) and (2), defined the ecosystem at two organizational levels, and may elaborate lower levels by the device of decomposing subsystems in the same manner. That is, if S may be defined at two levels, so may the elements of $\{S_i\}$, and the subsystems so defined, to any desired degree of fineness. Ultimately, it is necessary to end with a behavioral model for all subsystems, because it is this model that yields explicit form to the relational expressions.

Several points are of interest here. First, it is not clear that a hierarchical decomposition is always desirable. That is, a finer resolution may not best take the form of a decomposition of next most coarse form of interest. Hierarchical forms, however, have many advantages and will be used wherever possible. Second, it is quite clear that a uniform resolution is unnecessary. That is, a very coarse resolution model of one subsystem may be coupled with a fine resolution model of another, and such an arrangement will have many advantages. Not the least of these is the advantage of manageability. If we want to take a closeup view of some parts of the system, there is no reason to, and many reasons not to, look at the rest of the system at the

same degree of magnification. A hierarchical subsystem structure will be most conducive to a variable resolution, but again, it is not necessary.

Application of the General Theory to the Forest Ecosystem

With this introduction to the theoretical background, we can now take a look at the coarser ecosystem structures as we now perceive them. A diagrammatic convention is established which will be recognized as similar to Forrester's, but which differs in some important respects. Let boxes designate compartments (to be conceptualized as storage containers), let ovals or circles designate systems (or subsystems), and let diamonds designate a set of variables. Solid lines designate coupled flow variables and dotted lines represent control variables. As a convention, diamonds are eliminated from the flow couplings, as these variables are apparent from the context, but identification of control variables is important. Occasionally these are also eliminated from a figure to reduce clutter, and in the illustrations given here, most control paths are eliminated for the same reason.

In figure 1 is depicted a representation of a system as a whole, with inputs and outputs. At this level, the entire system (the forest ecosystem) is defined according to (1). In figure 2, the same system is elaborated by identification of major subsystems, the terrestrial biota, the aquatic biota and the hydrologic system. This involves definition of the system according to (2) and it should be emphasized at this point that there are very many ways in which this could be done.

Implementation of this form (fig. 2) requires decisions regarding boundaries and specifications of the nature of the couplings between subsystems. An example will illustrate both points. Consider the uptake of water by higher plants. Question: Do we wish to consider this water as having transferred

² After Koestler's "The Ghost in the Machine."

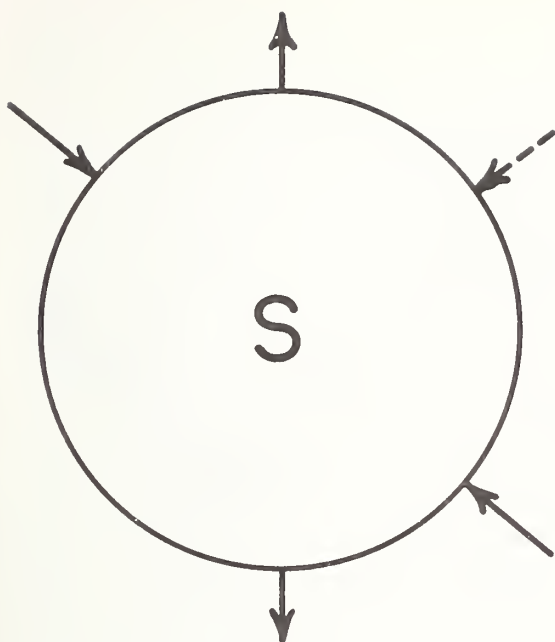


Figure 1. The system viewed as an object receiving inputs from the environment and producing outputs.

from the hydrologic system to the terrestrial biotic system? Or, will we let stored water remain in the hydrologic system? The answer to this is arbitrary and should be made on the basis of ultimate convenience. If the specification of couplings is simpler for one boundary definition than for another, then that boundary is preferred.

The nature of the couplings (or coupling variables) is also important. Suppose we let water enter the biotic system at the moment of uptake. Then the transfer of water from hydrologic to biotic depends on (1) the state of the hydrologic system (specifically, the amount and distribution of water available in the soil) and on (2) the biotic demand for water. These two variables must be identified as output variables of the respective systems in order to elaborate the transfer. It then is immaterial whether the calculation of transfer takes place in the hydrologic or the biotic system, but it seems appropriate that it be included in the latter as an uptake function. In fact, one can even leave the function of transfer outside both systems as a coupling

function, but this appears awkward.

Once all the couplings are identified and specified, then it is no longer necessary to consider one subsystem in elaborating the internal structure of another. The process of coupling specification effectively uncouples the system into subsystems, each of which can be developed independently, provided that the identified external variables of the subsystems are maintained.

I will use the word integrity in this context. Elaboration of the system at one level of organization is unrestricted so long as the integrity of the next higher level of organization is maintained. This does not appear at this writing to be a trivial problem, but the problem exists under any formulation of model structure and is well identified under the present structure, hence potentially manageable.

Decomposition of the Terrestrial Biotic System

With this background, I can develop further details of our present conceptualization. These results are presented in much greater detail in a project document titled "Modeling, Round One," prepared jointly by myself and a number of others in our program. This document summarizes a series of seminar-workshops in which we examined the definition of subsystems and the nature of their couplings. Reports of details of several subsystems are reported by others in this symposium. I will use several subsystems for illustration which are not treated elsewhere.

In figure 3 is seen a specification of primary subsystems of the terrestrial biotic system. These are not even, in the sense of evenness of importance, but rather are chosen to emphasize the relationships we wish to emphasize at this level. Only two compartments are specifically identified, the plant biomass (B. & S.) and the detritus (D.) compartments, with all others embedded in the respective systems. Identification of the biomass compartment forces explicit identification of a minor subsystem, litterfall. The

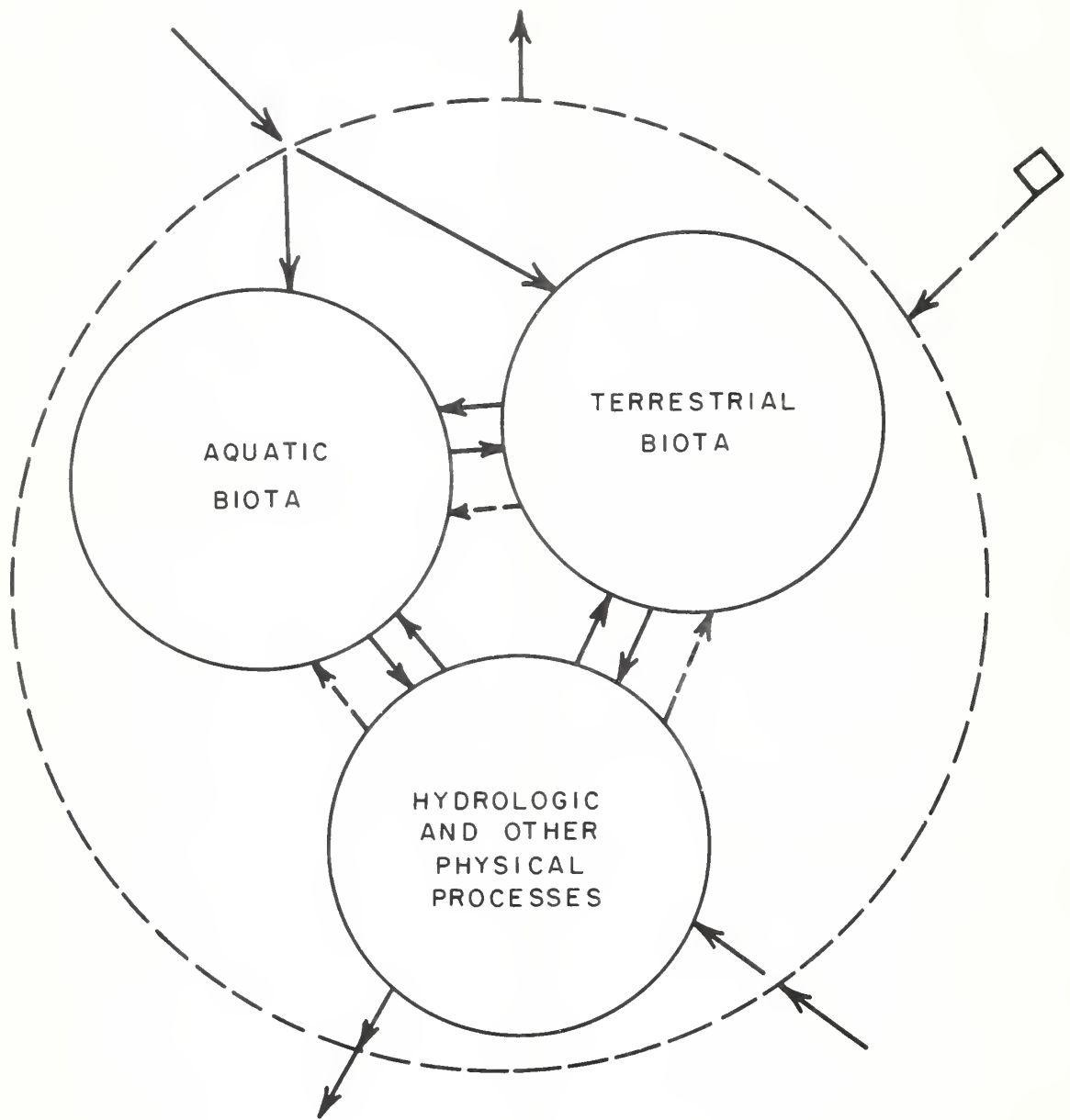


Figure 2. The major subsystems of a forest ecosystem. Specification of the coupling variables among the major subsystems allows independent development of their internal structure.

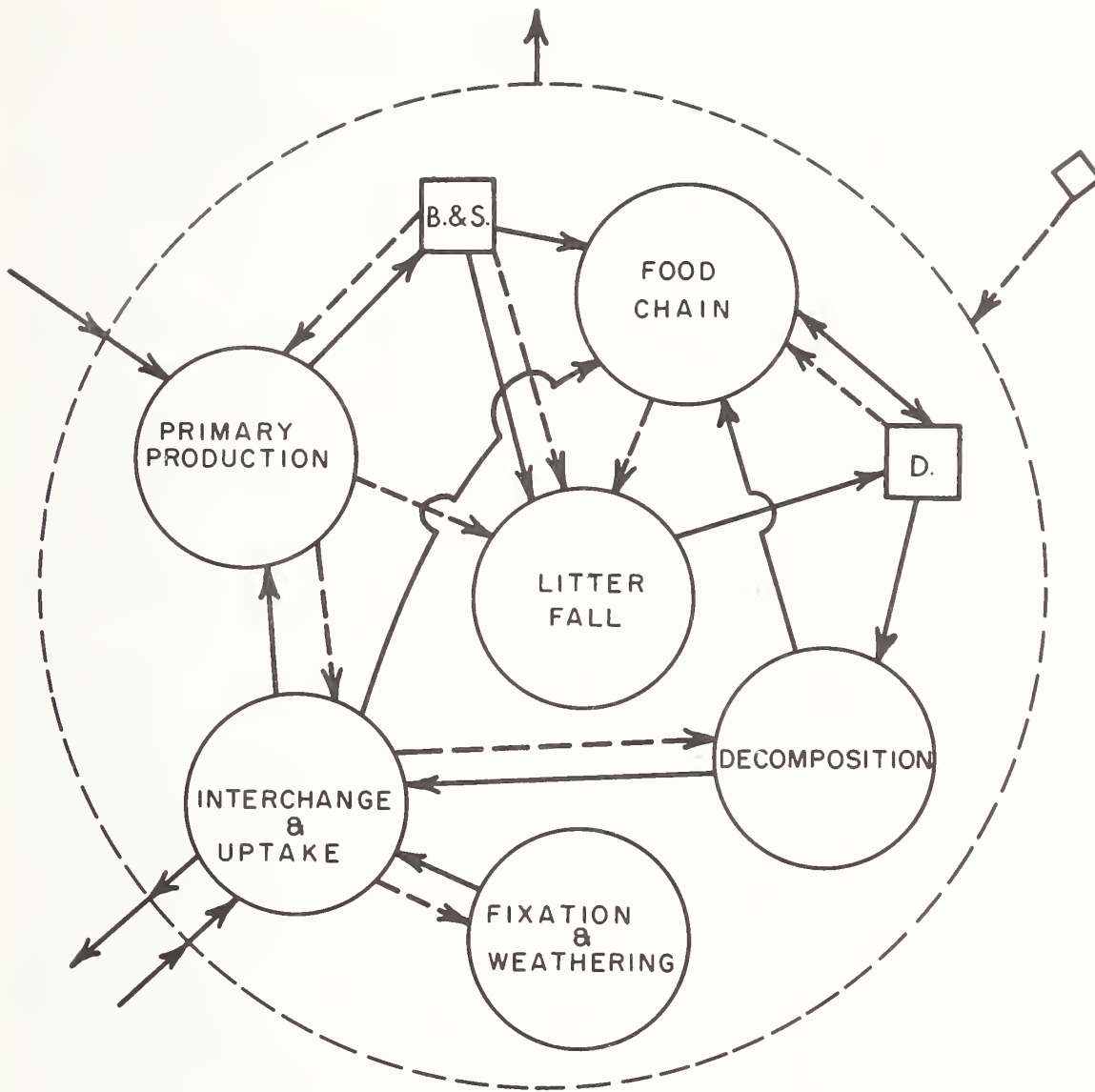


Figure 3. The December 1971 version of the subsystems of the Terrestrial Biotic System. The external variables of the whole system match those illustrated for this subsystem in figure 2.

traditional decomposition and fixation subsystem has been uncoupled into the three subsystems represented as Decomposition, Fixation and Weathering, and Interchange and Uptake (I-U).

The value of this formulation is several fold. First, we can recognize that this is a formal expression of generally held ideas, so that only the formality, and perhaps the

identification of the I-U process, is in any degree innovative. The formality gives substance to the concepts, and the formal U-C structure identifies the tasks facing us as we elaborate this structure. These tasks are: (1) specification of the coupling variables, (2) elaboration of internal structure of the subsystems, and (3) analysis and synthesis of behavior and properties of the systems and

subsystems as objects. In addition, the formal structure effectively partitions our effort and ensures that all bases are covered. Boundaries between subsystems and the appropriate coupling variables must be identified jointly by those responsible for the subsystems involved. After boundaries and coupling variables are agreed upon, then the activities of elaboration of internal structure are independent among subsystems. This is another expression of the earlier observation that identification of the couplings effectively uncouples the subsystems.

These values of the model formulation can be expressed as explication, conceptualization, and organization. Existing concepts are given explicit expression, new concepts are developed and research efforts are given structure and organization, all by the formal ecosystem model. The fact that the model structure is arbitrary in no way obviates these values. On the contrary, the arbitrariness of the model structure enhances these values, because as we proceed with the process of elaboration, and bring existing knowledge into sharper focus by the process of modeling, we are constantly forced into adjustments, reorientation, and reorganization.

Structures, like figure 3, are not meant to be permanent. They live and die like generations of insects. In fact, the insect analogy is quite appropriate for figure 3. This structure was conceptualized in the spring and early summer of 1971, during Round One. It developed underground, so to speak, all during the fall, undergoing several transitions, to emerge in December in the form presented. By mid-January 1972 this form had lived out its life and given birth to a new form which is yet in the larval stages and not ready for the light of day.

At the next lower organizational level, progress has been made in elaboration of the internal structure of the food chain subsystem and the I-U subsystem. The first is reported here by Strand and Nagel, but the second is not represented in this symposium and I would like to include a brief description of that subsystem as additional illustration of the way in which we are using the Universe-Coupling structure.

Figure 4 represents a model form dated back in 1971, which form has been replaced by a new but incompletely developed form, in accordance with the changes being made at the next lower resolution (fig. 3). However, figure 4 serves to illustrate the concept of the I-U process and, again, the point is made that this is developed more fully in the documents of Round One.

The I-U subsystem is postulated on the following statements:

1. If nutrients remain in soil solution, they must be lost to the system by soil and groundwater transport.
2. Nutrients must be in solution in order to be available to uptake.
3. Some microorganisms and some higher plants are "leaky."
4. It is concluded that a successful system must have a tightly coupled, highly interactive and buffered subsystem of nutrient interchange and uptake.

The modeling contribution here is the recognition (4) that the three stated features of the traditional processes of nutrient interchange are such that a successful terrestrial ecosystem (i.e., one which does not lose its nutrients downstream) must have a tightly coupled I-U subsystem. That is, the traditional study by individual process cannot possibly answer the questions we want to ask, unless we explicitly define the couplings. Coupling definition is difficult in a tightly coupled system, and appears exceedingly difficult in this one. The identified task is the conceptualization of properties and behavior of the I-U subsystem as a whole.

It is my very strong conclusion here that the Biome research effort should be re-oriented to accommodate the concept of the I-U subsystem. Present conceptualization and specification of that subsystem is yet very primitive and will receive considerable attention in the next year.

From the model structure point of view, the primary productivity subsystem is the least well defined in our model. This is, in part, because most of our research effort has been at lower organizational levels than is necessary for ecosystem models. It is a giant step from tree to community. The primary

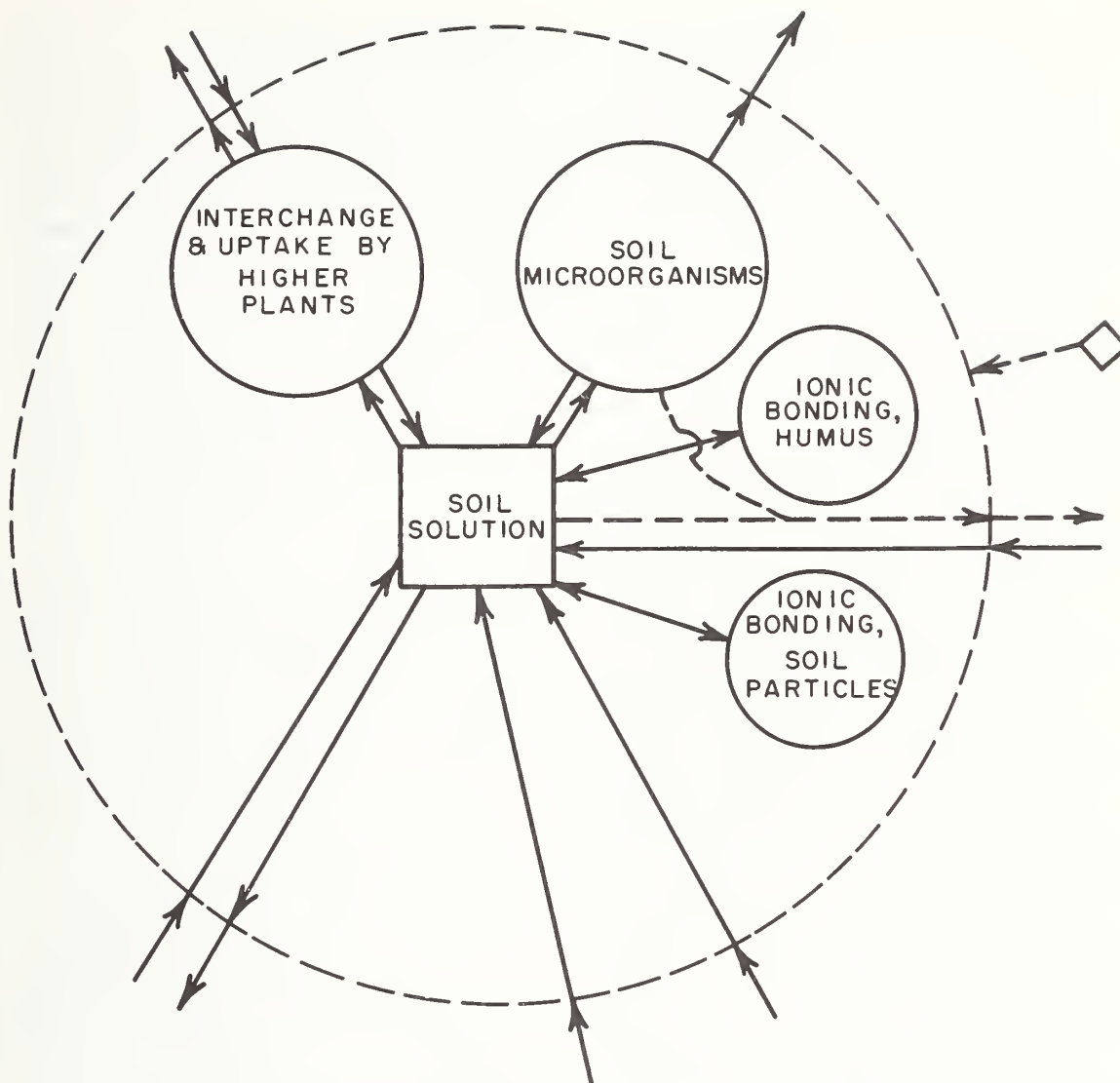


Figure 4. The December 1971 version of the subsystems of the Interchange and Uptake System. The external variables of the whole system match the couplings of the I-U subsystem of figure 3.

effort has been at the tree level (and below) and the model structures for the ecosystems are communities. The necessary effort here is apparent.

Representation of Spatial and Environmental Variation

The [Universe Coupling structure] is also appropriate to the problem of modeling a

heterogenous ecosystem. If the system is stratified into homogenous subsystems, identified by spatial or environmental criteria, then the models appropriate for each of the strata can be coupled together to form a model for the whole. This is the approach we have taken in our watersheds. A watershed is sufficiently variable, with regard to physical and biological processes, that we feel it is necessary to stratify so as to provide essential uniformity of processes within strata. The process of composition, of coupling the

several models together to form the model for the watershed as a whole, is the reverse of the decomposition process previously discussed. Now we are faced with the question of defining appropriate external variables of the watershed as an object after having initially defined the watershed as a collection of sub-objects.

These questions are obviously appropriate to consideration of a general model for, say, the entire H. J. Andrews Experimental Forest, or for the Coniferous Forest Biome, so that we consider them central to our overall objectives. By concentrating on the problem of stratifying a watershed, and on the problems of modeling the strata and the collective, we are attempting to devise strategies which will be useful in later extension of the modeling process.

It turns out that if we view the construction of strata in essentially the same perspective as the construction of subsystems in the U-C structure, the same general criteria hold. Generally speaking, subsystems (strata) should be constructed in such a manner that couplings are minimized (or simplified), and such that important processes are contained within the subsystems. This criterion is not always compatible with the second one, that strata should be environmentally homogeneous, within, and occasional conflicts arise. In any event, we are attempting hierarchical stratification of watersheds, with topographic features defining the primary strata and vegetation types the secondary, the two levels giving uncoupling and homogeneity, respectively.

Summary

Some of the ways in which the Universe-Coupling structure is being used in building a hierarchical, modular system of models for the Coniferous Biome have been discussed. These models are hierarchical by virtue of the identification of systems at one level of organization as subsystems of the systems defined at the next higher level. They are modular by virtue of the uncoupled nature; identification of the coupling variables at any level allows complete flexibility of subsystem

representation, provided that the integrity of the couplings is maintained.

A general criterion for constructing subsystems is provision of simple couplings among subsystems with tight relations contained within. This principle is violated quite badly when trophic levels are used for subsystem definition. An alternate structure for consumers is being investigated in our program, as reported in the paper by Strand and Nagel.

In applying the U-C structure to spatial units, another criterion is employed. Here it is desirable to provide homogeneity of environment and process within strata, with variation among strata of no concern. This criterion is sometimes in conflict with the first one of minimal couplings, so that compromises are necessary.

The paper has dealt primarily with aspects of structure and criteria for application of the structural form. Emphasis has been on the first two of the three tasks which the U-C structure defines, to wit: (1) specification of the coupling variables, (2) elaboration of internal structure of subsystems. The third task, analysis and synthesis of behavior of the subsystems as objects, is given little attention, but this probably is the most important, from the point of view of ecosystem theory. As mentioned earlier, the conceptualization of holistic system properties and behavior is poorly advanced. The U-C structure provides an excellent basis for the attempt to develop this concept.

One last point is made regarding the differences between the Universe-Coupling approach and the State Variable approach. Since the State Variable model can also assume hierarchical form (Goguen 1970), and under common explicit models of subsystem behavior the U-C model will reduce to a state variable model, one might question the practical validity of the distinction. Essentially, the differences are that one (U-C) is structure oriented and the other variable oriented and that one (U-C) is oriented simultaneously to holistic and mechanistic representation and the other solely to mechanism. In the application of ecosystem models so far produced, the state variable approach seems adequate,

except for the retention of fine detail. The tendency in constructing models on this base has been to develop fine resolution mechanistic models in which the variables defined at the finest resolution are in direct relation to all the other variables in the system. Variable orientation seems to lead to variable sanctity. One might make a case for the position that the state variable approach was developed by engineers who have no conceptualization problem. They know what their variables are, and the relations among them, and they are satisfied with mechanistic models.

The U-C structure is seen as a means of introducing holism, in addition to mechanism, into the model conceptualization process. By focusing on the subsystem structures, and by attempting to describe the behavior of the system and subsystems at all levels in terms of their behavior as objects, each system and subsystem is modeled at two levels, (1) holistically and (2) mechanistically in terms of the holistic behavior of its subsystems. This approach is held to be much more promising, from the point of view of development of ecosystem theory, than the currently popular approach.

Acknowledgments

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Hydrologic modeling in the Coniferous Forest Biome

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P. 6.

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Abstract

The objective of the hydrology program is to prepare a model which will provide predictions of the hydrologic state of a coniferous watershed at any desired time and in any desired place, where state is defined by the input needs of the other submodels or systems, particularly the producer and biogeochemical processes. Subsurface flow is the dominant runoff mechanism in coniferous watersheds and one of the least understood processes in hydrology. Research projects in hydrology seek to understand this process using three different techniques. One project relates subsurface flow to soil properties using direct measurement techniques. Another project approaches the problem using simulation techniques. The third project utilizes systems analysis and statistical decomposition of runoff events to make inferences about subsurface flow. These studies of hydrologic processes will be incorporated into a hydrologic model and linked to studies of other systems. The first step in linking our model with those of other groups is watershed stratification, a problem now solved by our modeling efforts.

Introduction

Water is an essential component of any ecosystem. In the Pacific Northwest, water is a dominant element. The coniferous forests of this region are noted as some of the best-watered terrestrial ecosystems in the United States; water is the major linkage which ties the terrestrial portion of the coniferous ecosystem to the aquatic portion.

Water performs several functions which

foster this linkage. Water must be viewed as a carrier. It carries organic and inorganic nutrients between the several compartments of the terrestrial portion of the ecosystem and from the terrestrial to the aquatic portion. Water also carries sediment from the terrestrial to the aquatic portion of the system.

Water must also be viewed as a nutrient itself. It is an essential component of most biologic processes. The availability of water in the soil governs both the initiation and termi-

nation of any process as well as the rate at which it proceeds.

Objective of the Hydrology Program

The objective of our program is to prepare a model which will provide predictions of the hydrologic state of a coniferous watershed at any desired time and in any desired place, where state is defined by the input needs of the other submodels or systems, particularly the producer and biogeochemical processes.

Structure of the Hydrology Modeling Effort

Our modeling effort is organized to pay particular attention to the many functions of water in the forest ecosystem. A generalized model for water flow through a forest system was conceptualized long ago. This model is often called the hydrologic cycle. Rothacher et al. (1967) showed for the H. J. Andrews Experimental Forest that water movement in the forest soil and evapotranspiration are the most significant processes governing water flow.

Our studies focus upon subsurface water movement. One project measures subsurface flow directly in the study watershed. Another study is a computer simulation of a watershed. This approach will provide yet another avenue for assessing soil moisture and the subsurface flow of water. The simulation model will be calibrated using 14 years of record on watershed 2. Then the model will be verified with the data available on watershed 10. A third project seeks to develop techniques for predicting the subsurface flow component using a systems analysis technique for statistical decomposition of the hydrograph into its components. Other studies will contribute submodels to the simulation of the hydrologic system. The work of the Primary Producer group on a transpiration model as well as the work of the Meteorology group on an evapotranspiration model will aid our modeling effort significantly.

We are concurrently working toward a more spatially refined model, the character of

which is determined as much by biologic as hydrologic constraints. Our latest efforts have focused upon devising a system for stratification of watershed 10 which is amenable to both hydrologic and biologic models.

Other hydrology projects are included in the biome effort. We hope to provide hydrologic measurements as a part of the work at Findley Lake and the evapotranspiration study at the Thompson site. We shall soon begin to solicit and organize available data from coniferous watersheds throughout the West in anticipation of extrapolating our model to other ecosystems.

This has provided a broad overall view of the Coniferous Biome Hydrology Program—its structure to achieve a better understanding of water flow through the ecosystem and its interaction with other system components. A more detailed description of the hydrology efforts follows. Each project focuses upon evaluating water flow in a forested watershed. Analytical techniques vary between projects, but the ultimate goal of modeling subsurface flow mechanisms and watershed response links all projects together.

Subsurface Movement of Water on Steep, Forested Slopes¹

With the exception of stream channel interception, the hydrographs of watersheds in the forested, steep topography of western Oregon reflect overall subsurface movement of water. Watershed response is rapid but without surface runoff (Barnett 1963, Rothacher et al. 1967). Although subsurface flow is by far the major component of the hydrograph, virtually nothing is known about the process on steep slopes. The objective in our study is to characterize the subsurface movement of water in steeply forested topography.

¹ Authored by R. Dennis Harr, Assistant Professor, Oregon State University, Corvallis.

The study areas are located at several of the lower watersheds in the H. J. Andrews Experimental Forest near Blue River, Oregon. Vegetation is typical of the low-elevation Douglas-fir forest. Study slopes average about 75 percent. Soil depth is variable with maximum depths in excess of 5 meters. Because of high porosities (70-80 percent) and large proportions of macropores, these soils drain rapidly. Permeabilities of 5,000 and 900 mm per hour have been noted on nearby watersheds for surface soil and subsoil, respectively (Dyrness 1969).

Methods

Initial investigations are being directed toward describing the physical properties of the porous medium through which water moves on its way to a stream. These field and laboratory investigations will indicate where water movement most likely occurs.

Drilling with a portable power drill will follow a grid pattern over a small stream-to-ridge portion of slope. At each grid point soil depth, depth and thickness of saprolite, and depth to unweathered bedrock will be determined. Additional drilling between initial grid points will indicate in more detail the surface contour of the impermeable parent material. Aluminum tubing placed in each hole will provide access for measurement of ground-water level or soil moisture content.

In the laboratory, undisturbed soil cores taken from various depths in soil pits located over the study area are being analyzed. Such properties as porosity, pore-size distribution, stone content, permeability, and moisture retention characteristics are being evaluated.

The type and amount of measurements to be made during and following winter storm events in 1972-73 will depend on the information gathered during initial field and laboratory investigations now underway. Anticipated measurements include soil moisture content, vertical and lateral extent of saturated flow, soil moisture tension, precipitation, and water outflow from the base of the slope. Drilling and tracer studies will attempt to define the source area for this

water.

Preliminary Results

Although the study has just recently begun, certain observations have provided qualitative information concerning the subsurface flow process on steep slopes. Precipitation moves downward under the influence of gravity until this movement is obstructed. In some parts of the study area this obstruction may be caused by rock fragments which cause shallow, localized saturation as evidenced in several soil pits during a period of heavy rain. Where rock fragments are not present, downward movement of water continues until the relatively impermeable parent material is reached. Here saturation occurs, flow acquires a horizontal component, and water begins moving toward the stream.

At some point on the slope this saturated flow is concentrated into pipelike subsurface channels. The cause of this concentration is unknown but could conceivably result from the microrelief of the impermeable material, from bedrock fractures, or from decayed root channels. At the toe of the slope the channels are spaced about 1-6 meters apart. They lie on the bedrock surface and appear associated with surface micro-relief. Shapes of their cross sections range from circular to flat rectangular. Width is also variable, ranging from 1 centimeter to about a meter. Where these channels discharge into the stream channel, they are separated by soil which may contain a shallow saturated lower layer from which seepage occurs. Water velocity of the seepage appears to be several orders of magnitude lower than that of the subsurface channels. The latter accounts for the greatest portion of stormflow.

The subsurface channels evident at the toe of the study slopes may be outlets of a subsurface drainage system much like that described for other humid areas (Jones 1971). Water can be observed discharging from such channels in roadcuts and recent soil slumps at various slope positions in the vicinity of the study area. Such a subsurface drainage system could account for the rapid hydrologic response of these steep slopes.

*Computer Simulation of Forest Watershed Hydrology*²

A hydrologist is often faced with the need to predict system responses under various possible management alternatives. One approach to this problem is to apply the technique of computer simulation, whereby a quantitative mathematical model is developed for investigating and predicting the behavior of the system. In this study, a computer model is being developed to simulate the hydrologic responses of a forest watershed, emphasizing the measurable variables related to the plant communities and soil types of the watershed. The model represents the inter-related processes of the system by functions which describe the different components of physical and biological phenomena in a watershed.

Scope and Objectives of the Simulation Study

In the first phase of the study, the scope is being limited to the formulation of a fundamental model of watershed hydrology which takes precipitation as the basic input and evapotranspiration and streamflow as outputs of the system. The various component processes within the system are linked by the conservation of mass principle. Depending upon energy levels, water can vary among its solid, liquid, and vapor forms; hence, the energy budget is used as an auxiliary tool for maintaining the water balance. That aspect of the system involving water as a carrier of nutrients and sediments will be examined in a subsequent phase of the study. Under this next phase a water quality submodel will be formulated and added to the quantity model now being developed.

The specific objectives of the current phase of the study are stated as follows:

1. To develop and verify (calibrate and test) a hydrologic simulation model for a small forested subwatershed on the H. J. Andrews Experimental Forest.
2. To estimate through model sensitivity studies the relative importance of various processes within the hydrologic system of the model, with particular emphasis on evaluating the soil moisture and inter-flow components.

Hydrologic System Models

Several hydrologic simulation models are currently available. Examples which might be cited include Crawford and Linsley (1964), Sittner et al. (1969), and Riley et al. (1966). However, in order to meet the needs of this study all existing models require some modifications and further development. Therefore, on the basis of previous work at Utah State University a computer model is being developed to simulate the hydrologic behavior of forest watersheds. The model will be applicable to a wide variety of geographical areas and management problems. In this study, data from watershed 2 on the H. J. Andrews Experimental Forest will be used to demonstrate the utility of the model. Figure 1 summarizes the geophysical features of the study area (Rothacher et al. 1967). Data requirements include air temperature, precipitation, runoff hydrographs, and characteristics of the watershed (average slope, degree and aspect, vegetative cover, density of vegetative cover, soil moisture holding characteristics, and drainage density). Other observed records, such as snow depth, soil moisture content will be used to check the performance of the model in simulating various component processes of the system.

Figure 2 illustrates the various component processes represented in this model, with the boxes representing storage locations and the lines transfer functions. Under this study, the hydrology of the drainage area will be synthesized first as a lumped parameter model in which the entire watershed area is considered as a single space unit. On this basis, a dis-

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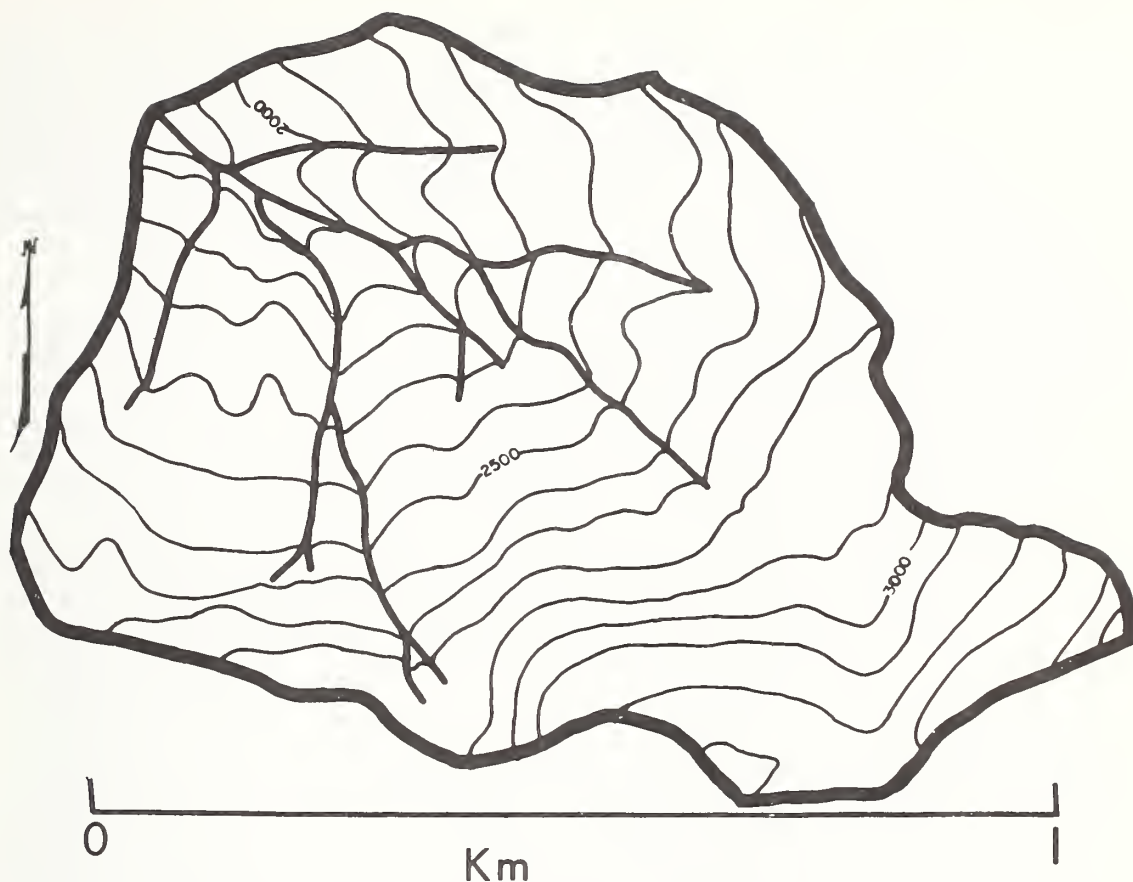


Figure 1. Watershed 2, H. J. Andrews Experimental Forest, Oregon. Area: 60.3 hectares; aspect: NW; average slope (percent): 61.1; elevation min.: 526 m; elevation max.: 1,078 m; main channel length: 1,108 m; drainage density: 4.3 km/km²; precipitation (1952-62): 2,400 mm/yr; runoff (1953-62): 1,560 mm/yr; average evapotranspiration (1959-62): 540 mm/yr.

tributed parameter model will be developed in which the watershed will be divided into four space units, roughly corresponding to sub-watersheds within the area. The model will compute continuous daily streamflow for each subarea and route the contribution of each down the streams to the gaging station, where the computed and observed discharges will be compared. Other important output functions from the model will include soil moisture, actual evapotranspiration, and snow depth. Several of the component processes which are illustrated by figure 2 are discussed in the following sections.

Interception

Interception is the part of precipitation

that is caught temporarily by forest canopies and then redistributed either to the atmosphere by evaporation or sublimation or to the forest floor. The amount of interception depends upon storm size and intensity, and canopy type and density. A report by Rothacher (1963) showed that throughfall in the study area was related to storm size by the equation:

$$\text{Throughfall} = 0.8311 \times (\text{gross precipitation}) - 0.117 \quad (1)$$

In equation 1 throughfall is, of course, bounded by the condition that it must be greater than or equal to zero. Although larger amounts of snow may be temporarily intercepted than rain, there is strong evidence that most intercepted snow ultimately falls and becomes part of the snowpack.

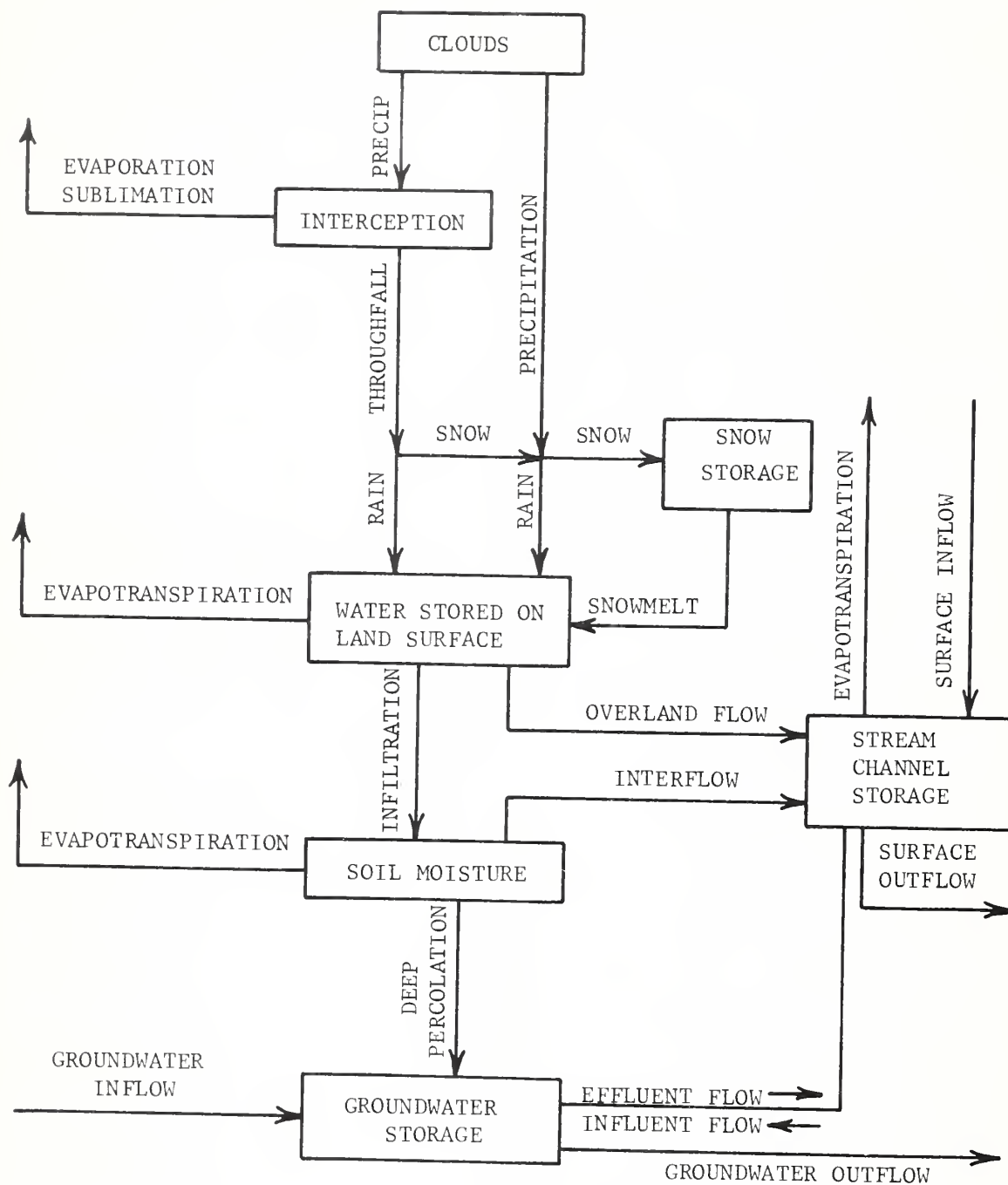


Figure 2. A flow diagram of the hydrologic system within a typical watershed area.

An alternative way of considering interception quantities in a model is to express interception rate as a decaying function of time limited by an average interception storage capacity for the watershed canopy. This approach was incorporated into a watershed simulation model by Riley et al. (1966).

Snow Storage and Melt

Forms of Precipitation

Only two forms of precipitation, rain and snow, are considered in this study, with a surface air temperature criterion being applied to establish the occurrence of these two forms. Figure 3 (U.S. Army Corps of Engineers 1956) shows that at a temperature of 1.5°C there is a 50-percent chance that the precipitation will be in the form of snow. A straight-line fit to figure 3 is used to deter-

mine the portion of rain in a given day according to the following equation.

$$R = P \cdot \frac{T_a - T_s}{T_r - T_s} \quad (2)$$

in which

- R = estimated portion of total daily precipitation occurring as rain
- P = total daily precipitation
- T_a = mean daily surface air temperature
- T_s = mean daily air temperature below which all precipitation is assumed to occur as snow
- T_r = mean daily air temperature above which all precipitation is assumed to occur as rain

Precipitation falling as snow will be accumulated on the watershed until air temperatures rise sufficiently above the freezing point to initiate snowmelt.

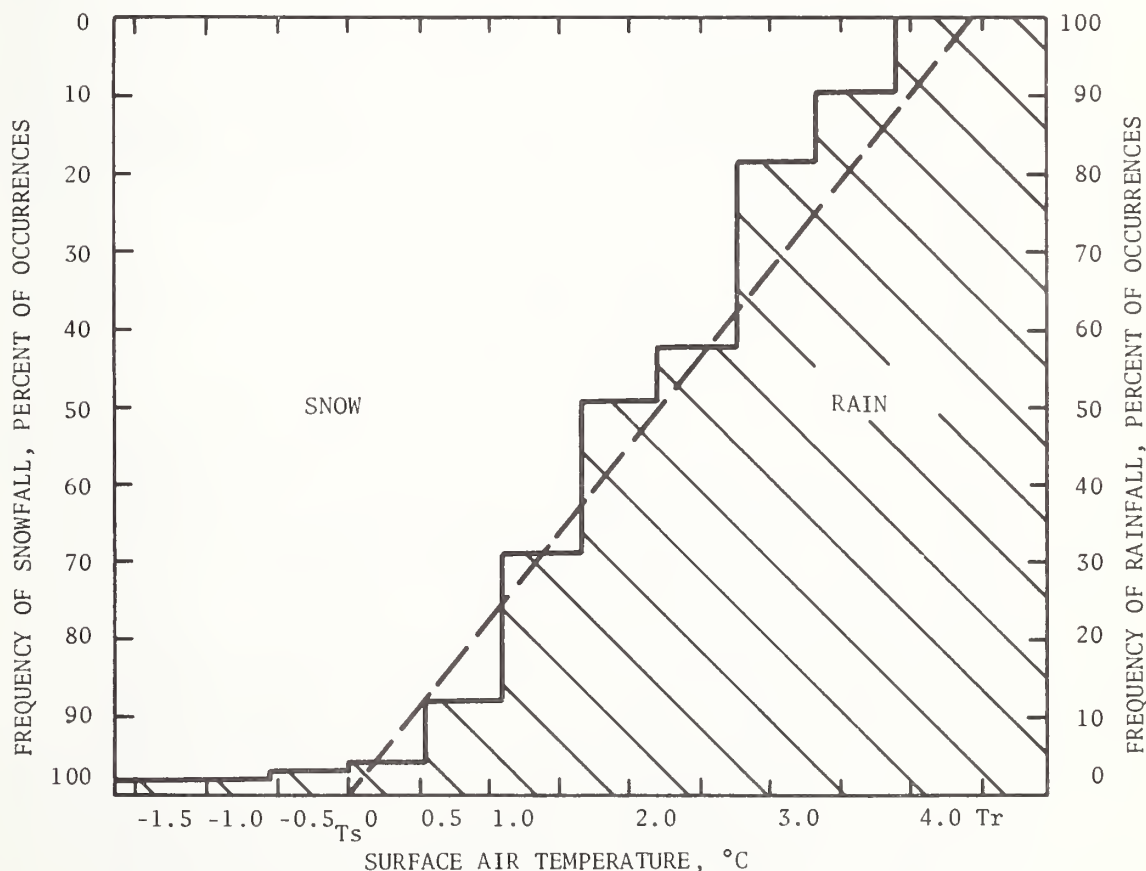


Figure 3. Frequency distribution of precipitation in rain and snow forms.

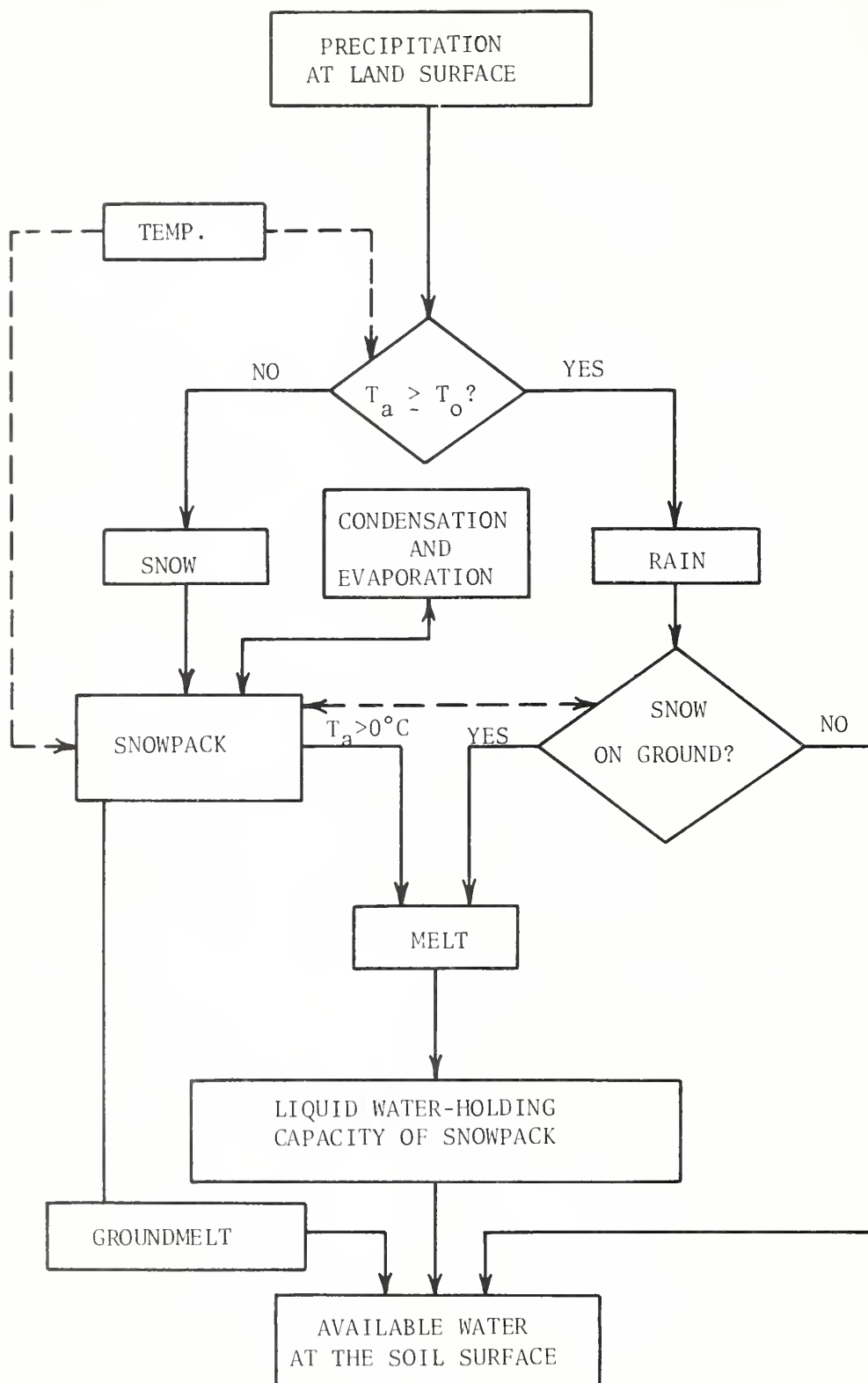


Figure 4. A flow chart of the snow accumulation and ablation processes.

Snowmelt

A flow chart of the snow accumulation and ablation processes is shown by figure 4. Rate of snowmelt depends primarily upon the rate of energy input to the snowpack. However, both the complex nature of snowmelt and data limitations prevent a strictly analytical approach to the simulation of this process, and air temperatures are frequently applied as an index of available energy. Examples of researchers who have used this approach are Pysklywec et al. (1968), Anderson and Crawford (1964), Amorocho and Espildora (1966), and Eggleston et al. (1971). Because temperature data are the only indicators of energy levels available on watershed 2, a degree-day approach based upon the work of Eggleston et al. (1971) will be used in the model of this study to represent the snowmelt process at the surface of the snowpack. This component submodel includes mathematical relationships for various phenomena involved in the snowmelt process. The submodel is applicable to any geographic location by determining appropriate constants for certain relationships through a verification procedure. The relationship for surface melt rate is expressed as follows:

$$M_{rs} = k_m k_v \frac{RI_s}{RI_h} T_a (1 - A) + T_a \frac{P_{rg}}{80} \quad (3)$$

in which

- k_m = a constant of proportionality
- k_v = vegetation transmission coefficient for radiation
- RI_h = radiation index for a horizontal surface at the same latitude as the particular watershed or zone under study
- RI_s = radiation index for a particular watershed zone possessing a known degree and aspect of slope
- T_a = surface air temperature in °C
- A = albedo, or reflectivity, of the snow-pack surface
- P_{rg} = precipitation reaching the snow surface in the form of rain, in centimeters

Infiltration

Rates of water supply on the ground surface, whether in the form of rainfall minus interception or snowmelt, must exceed infiltration rates before any surface runoff occurs. The infiltration rate depends on the physical and moisture characteristics of the soil, as well as the surface organic conditions, and it is often expressed in the form of Horton's exponential equation. However, the soils of watershed 2 are very porous and no overland flow has been observed. Thus, all precipitation reaching the ground surface is assumed to infiltrate into the soil and to move to the stream channels as subsurface flow.

Soil Moisture

Soils on the study watershed are relatively deep and have a high porosity. Data on the physical properties of the watershed soils are available (Rothacher et al. 1967), and this information will be used to determine the soil moisture holding characteristics.

The computer model allows infiltrating water to satisfy first the available moisture holding capacity of the soil within the root zone of the forest canopy. When the available soil moisture holding capacity is reached, additional infiltration is assumed to percolate by gravitation either somewhat laterally within the root zone or downward to deeper soil zones. Water which moves laterally usually reaches a surface channel within a relatively short period of time, whereas deep percolation moves from the watershed more slowly and sustains streamflow during dry seasons. From preliminary studies (Rothacher et al. 1967), approximately 87 percent of the total annual precipitation reaches the ground surface, and about 75 percent of this quantity becomes surface runoff. From an analysis of streamflow hydrographs it is estimated that about 10 percent of the runoff comes from baseflow, which is contributed from deep percolation. Thus, of the average annual precipitation of 2,400 mm which falls on the watershed approximately 2,100 mm enter the soil, 440 mm are abstracted by evapotranspiration, and the remaining 1,660 mm leave

the watershed as surface runoff, with 170 mm of this quantity occurring as baseflow. The soil moisture content computed by the model will be checked with observed data.

Evapotranspiration

Factors affecting evapotranspiration include temperature, solar radiation, wind, humidity, and consumptive use by plants. However, only temperature and humidity data are available for the watershed. Among the commonly used evapotranspiration equations (Veihmeyer 1964), the Penman equation is perhaps the most rational, but the data requirements are extensive. For this reason, the modified Hargreaves (Veihmeyer 1964), will be used in this study. The equation is stated as follows.

$$U = \sum K d (0.38 - 0.0038h) T_a \quad (4)$$

in which

- U = the daily potential evapotranspiration in centimeters
- d = the daily daytime coefficient dependent upon latitude
- h = the mean daily relative humidity at noon
- T_a = the mean daily surface air temperature in °C
- K = a monthly consumptive use coefficient which is dependent upon plant related characteristics, such as species, growth stage, and density on the watershed

The influence of soil water on evapotranspiration has been the subject of much research and discussion. It is now generally recognized that there is some reduction in evapotranspiration rate as the quantity of water within the root zone decreases. In this study it will be assumed that evapotranspiration occurs at the potential rate through a certain range of the available soil moisture. A critical moisture level is then reached at which actual transpiration begins to lag behind the potential rate. Within this range of the available soil moisture the relationship between available water content and transpiration rate will be assumed to be virtually linear. Thus,

$$E = U, [M_{es} \leq M_s(t) \leq M_{cs}] \quad (5)$$

in which

- E = daily evapotranspiration adjusted for the influence of soil moisture levels
- M_s = quantity of water stored within the root zone and available for plant use at any time, t
- M_{es} = limiting root zone available moisture content below which soil moisture tensions reduce evapotranspiration rates
- M_{cs} = root zone storage capacity of water available to plants

$$E = U \frac{M_s(t)}{M_{es}}, [M_{es} > M_s(t) \geq 0] \quad (6)$$

Considering the pressure effect, the total rate of gravity water storage depletion through both interflow and deep percolation is assumed to be directly proportional to the quantity of water in this form of storage remaining in the soil profile at any particular time. The interflow portion of this depletion, N_r, will be expressed as follows:

$$N_r(t) = K_i \frac{dG_s}{dt} = K_i (K_g G_s(t)) \quad (7)$$

in which

- K_i = interflow depletion coefficient
- K_g = gravity water depletion coefficient

That is, $N_r = K_i K_g G_s(0) e^{-K_g t}$, in which gravity storage at time, t = 0 is represented by G_s(0) and no input to G_s is assumed to occur between t = 0 and any other time, t. It is estimated that on watershed 2 about 90 percent of the gravity water storage leaves the area as interflow, in which case K_iK_g = 0.9.

Groundwater

Water enters groundwater storage as deep percolation from the overlying plant root zone. The rate of deep percolation, G_r, is numerically equal to the total rate of gravity water depletion within the root zone less the interflow rate. Thus,

$$G_r = (1 - K_i) \frac{d G_s}{dt} \quad (9)$$

By integrating equation 9 over a specific time period the accumulated inflow to the groundwater basin, G_w , is estimated for this time period.

$$G_w = \int_0^t (1 - K_i) \frac{d G_s}{dt} dt \quad (10)$$

If the groundwater basin is considered as a linear reservoir, the outflow rate is given by the expression

$$Q_{rg} = K_b G_w \quad (11)$$

in which

K_b = a coefficient which is estimated from dry season streamflow hydrographs

Q_{rg} = the outflow rate from the groundwater reservoir

By combining equations 9 and 11, the net rate of storage change within the groundwater basin is derived as

$$G_r - Q_{rg} = \frac{d G_w}{dt} \quad (12)$$

By substituting equation 11 into equation 12 and rearranging terms, the following relationship is obtained.

$$\frac{d Q_{rg}}{dt} = K_b [G_r(t) - Q_{rg}(t)] \quad (13)$$

The rate of discharge from the groundwater basin as baseflow is obtained by solving equation 13 for Q_{rg} .

Runoff

The possible sources of streamflow at any reach within a channel are overland flow (surface runoff), interflow, groundwater, and upstream input. Manning's equation is usually applied to compute overland and channel flow rates at any point. Under conditions on watershed 2, however, surface runoff does not occur, and channel routing on a daily time increment

is not significant. Therefore, runoff rates at the stream gage are given by summing the interflow and groundwater discharge rates.

Model Verification

Model verification includes calibration of the model parameters to a particular area, testing the sufficiency of processes defined in the model, and examining the prediction performance of the model. A self-calibration subroutine will be included in the model whereby the program will search for optimal model parameter values. Under this procedure each water year is used as a unit for optimization and the objective function is to minimize the variance between observed and computed streamflow (Shih 1971). The sufficiency of processes defined in the model is reflected in the dispersion of parameter values resulting from each year of calibration. After the model is calibrated, those years of data which were not used for calibration are used to examine the confidence level of predictions by the model. A flow diagram of the model verification procedure is shown by figure 5.

Model Parameters

Model parameters are the coefficients used in defining the processes which have not been accurately measured or which cannot be directly measured. By establishing the values of these coefficients the general model is fitted to the hydrologic system of a specific watershed. Depending upon the resolution of the model and the availability of data, the number of parameters to be calibrated may vary. In order to avoid using a large number of degrees of freedom in the calibration process and to save computation time, the number of model parameters should be kept as few as possible. In this study, the preliminary model parameters to be calibrated are interception storage capacity (S_I), snowmelt coefficient (K_S), soil moisture retention capacity (M_{CS}), gravity water depletion coefficient (K_g), and groundwater recession coefficient (K_b).

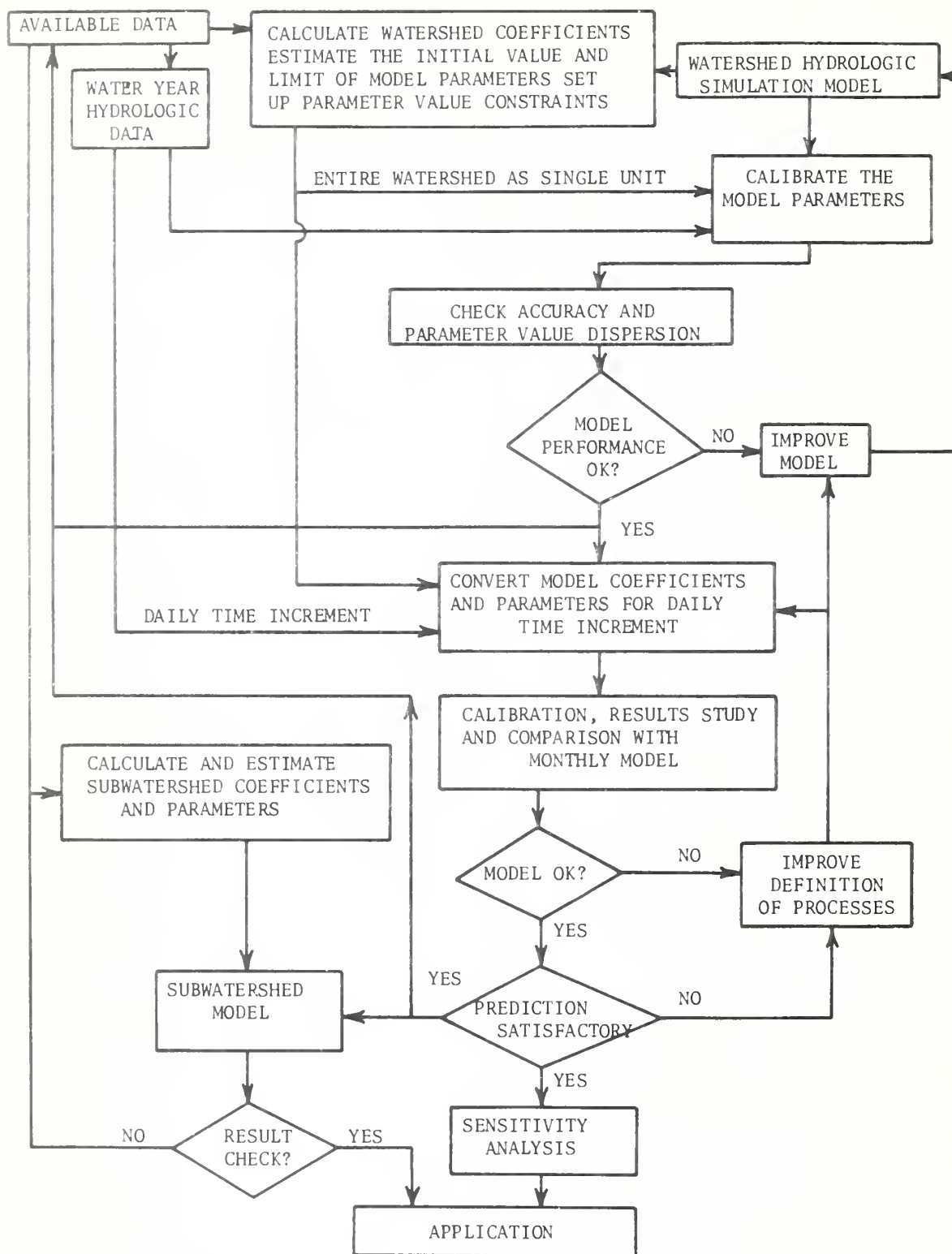


Figure 5. Flow diagram for verification procedure.

Calibration of Parameters

In general, it is anticipated that realistic parameter values are established through the calibration procedure. However, when streamflow is the only available component for checking the model, it is possible that several combinations of parameter values will yield satisfactory agreement between observed and computed outflow hydrographs. The problem of establishing unique parameter values is approached on the basis of hydrologic judgment and by using "interior" observations, such as snow depth and soil moisture, as check points on model performance. Other ways of testing the model include the time distribution of output quantities, such as streamflow, and known (or estimated) monthly or annual quantities. For example, for watershed 2 it is estimated that interception storage is about 0.5 cm, and total interception amounts to approximately 17 percent of the annual precipitation.

Under the self-calibration technique model parameter values are altered or perturbed in a random sequence and the resulting changes in the objective function are examined (Shih 1971). A computer flow chart for the calibration subroutine is shown by figure 6. The entire program model, including the calibration subroutine, will be synthesized on a hybrid computer.

Sensitivity and Management Studies

Sensitivity

A sensitivity analysis is performed by changing one system variable while holding the remaining variables constant and noting the changes in the model output functions. If small changes in a particular system parameter induce large changes in the output or response function, the system is said to be sensitive to that parameter. Thus, through sensitivity analyses it is possible to establish the relative importance with respect to system response of various system processes and input functions. This kind of information is useful from the standpoint of system management, system modeling, and the assignment of priorities in the collection of field data. Under this study,

the verified model will be used to perform various sensitivity analyses for the hydrologic system of watershed 2.

Management

Opportunities for management of a forest watershed are widely varied, and range from changes in logging practices to forms of soil treatment. Actual implementation of a management scheme depends upon benefits gained as compared with possible disbenefits. The simulation model developed under this study will not make direct comparisons of benefits and disadvantages, but will predict changes in the system output associated with given management alternatives. Under this study the capability of the model will be demonstrated for rapidly testing many possible management alternatives.

Much of the work discussed by this paper is based upon past developments in watershed simulation at Utah State University. Hydrologic modeling of the H. J. Andrews Experimental Forest for Coniferous Forest Biome has just begun, and the preceding discussion has been influenced by a consideration of particular conditions in the study area. However, the model will be fundamental in concept, and therefore generally applicable in a geographic sense. Whenever feasible, the model will use basic equations which are valid for short time intervals to define the various processes in the model. The output will then be summed for application to daily or longer time increments. For example, Horton's infiltration equation is applicable in minute units, but by summing these quantities, the model is capable of calculating equivalent daily infiltration rates. For the area under this study, however, it is assumed that water supply rates at the ground surface do not exceed infiltration capacities, so that surface runoff does not occur, thus considerably simplifying the model calibration process.

System functions which are important to forest management and other aspects of the total project include evapotranspiration and soil moisture. These functions, along with streamflow, will be estimated by the model for use in other parts of the total system

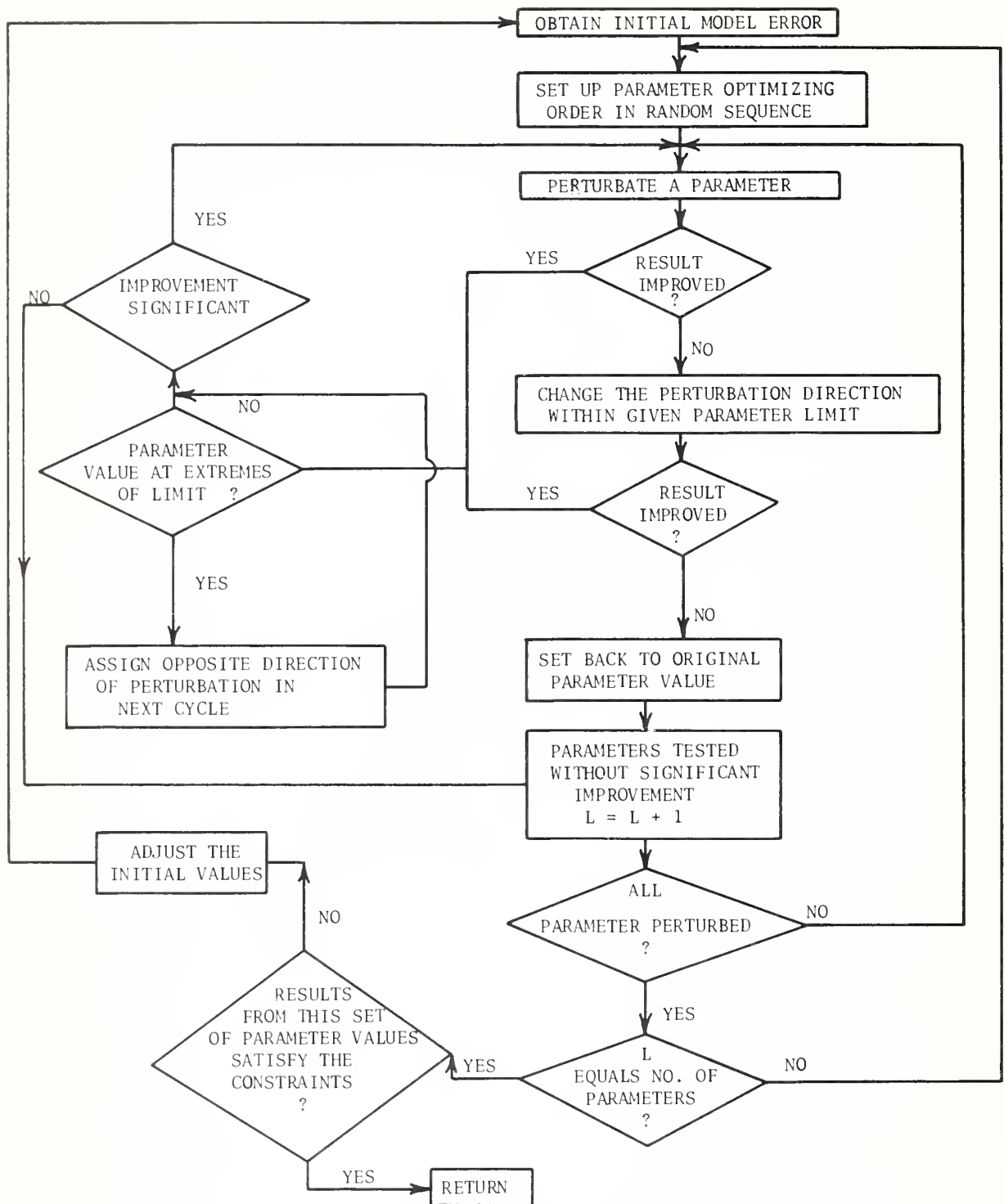


Figure 6. Flow chart for the model calibration.

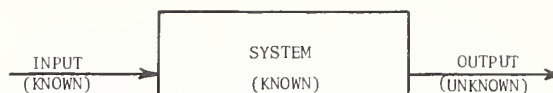
model being developed under the Coniferous Biome Program. The important underlying feature throughout the entire study will be that all of the separately described hydrologic processes and phenomena are interlinked into a total system. Thus, from the model, hopefully, it will be possible to evaluate the relative importance of the various items, explore critical areas where data and perhaps theory are lacking, and finally establish guidelines for the improved management of forest watersheds.

Hydrologic Systems Analysis³

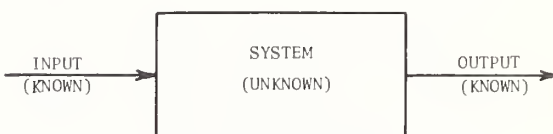
The purpose of this research is to devise a technique for statistical decomposition of a hydrologic event such that system processes such as precipitation, subsurface flow, and evapotranspiration, which contribute to the observed streamflow can be separated and described. This technique will therefore provide one more avenue for determination of the subsurface flow process on forest soils. The technique chosen for this research is a form of systems analysis.

Systems, Definitions and Basic Principles

System may be defined as an aggregate of physical parts that do not change with time, operating on an input to produce an output, both being functions of time. The simplified representation of a watershed, given in figure 2, can be considered as a system whose input is precipitation and runoff its output. System "synthesis" is a technique employed when the system is known in terms of a mathematical equation; the objective is to determine the nature of the output for any class of input (fig. 7). In system "analysis" a system response function or kernel which best describes a given input-output pair is derived (fig. 7). The term "best" implies that the derived kernels are not unique. Combinations of both techniques can be used for the solution of hydrologic problems. A system can



(A) SYSTEM SYNTHESIS



(B) SYSTEM ANALYSIS



(C) MULTI-INPUT/OUTPUT SYSTEM

Figure 7. Illustration of systems.

have one input and one output or many inputs and outputs (fig. 7). A system is "lumped parameter" if input and output are functions of a single variable. Otherwise, the system is of the "distributed parameter" type. If the system response at any time, due to a given input, is uniquely determined, the system is said to be "deterministic." If the system response is subject to uncertain influences, the system is "stochastic or probabilistic."

A quantity z is a "functional" for the function $x(t)$ in the interval (a,b) , if it depends upon all values taken by $x(t)$, when t varies in the interval (a,b) . An illustration of a functional is given in figure 8. The output of a system is a functional of the input and, for the same reason, runoff is a functional of precipitation. A system is "time invariant" if it does not change with time. Such systems can be represented by functionals. "Physically realizable" is a system whose output at time t depends only upon past values of the input.

³ Authored by Z. G. Papazafiriou, Research Associate, and R. H. Burgy, Professor, University of California, Davis.

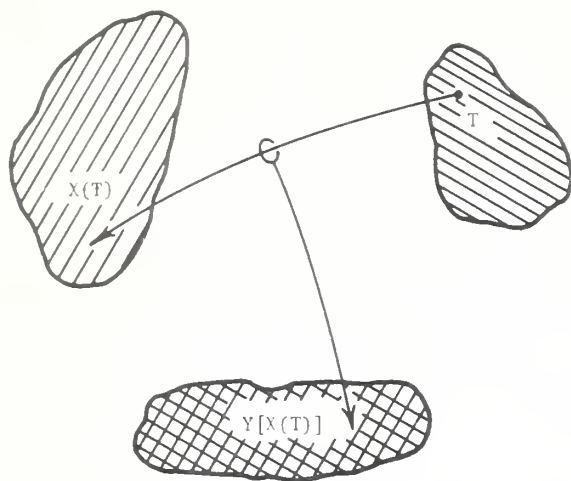


Figure 8. Demonstration of a functional.

Hydrologic systems are physically realizable since their outputs (runoff) at time t depend only on the past values of their inputs (precipitation). The "memory" of a system is the time period between some past time and the present for which the output depends only upon the input. If the output depends only on the present value of the input, the system is said to be a "no-memory" system. If the output of a time invariant system is analytic about zero input at some time t_0 , the system is "analytic". Analyticity is very important, since if a system is analytic, its output can be expanded in Volterra series. Hydrologic systems are assumed to be analytic.

A deterministic system \underline{H} is said to be "linear," if given the inputs $X_1(t)$ and $X_2(t)$ such that

$$y_1(t) = \underline{H} [AX_1(t)] \quad (14)$$

$$y_2(t) = \underline{H} [BX_2(t)] \quad (15)$$

implies that

$$\begin{aligned} y_1(t) + y_2(t) &= y[X(t)] \\ &= \underline{H} [AX_1(t) + BX_2(t)] \\ &= A\underline{H} [X_1(t)] + B\underline{H} [X_2(t)] \end{aligned} \quad (16)$$

that is, in a linear system, each member of a sequence of input values influences the output independently of every other. This is the well known principle of superposition. If a system does not satisfy the above condition it is said to be "nonlinear." A nonlinear system

can be almost linear, but there is no linear system which can be almost nonlinear. In general, linearity is a limiting case of nonlinearity. Therefore, any theory or technique adequate for a general nonlinear system is equally adequate for linear systems.

Deterministic Linear Hydrologic Systems

The theory behind most linear methods can be generalized in the following manner. Suppose that s and σ are continuous variables representing position in space, and t and τ define position in time. Consider the linear P. D. E. of the general form

$$L[g(s,t)] = f(s,t) \quad (17)$$

where L is linear P. D. operator of arbitrary order, and $g(s,t)$ some function which satisfies equation 17 within a certain region R . Given the appropriate homogeneous boundary conditions along R , the solution of equation 17 can be written according to Hildebrand (1958) as

$$g(s,t) = \iint_R G(s,t; \sigma, \tau) f(\sigma, \tau) d\sigma d\tau \quad (18)$$

If

$$f(s,t) = f_s(s) f_t(t) \quad (19)$$

equation 18 can be written in the form

$$g(s,t) = \int f(\tau) \left[\int_s G(s,t; \sigma, \tau) d\sigma \right] d\tau \quad (20)$$

If $f_s(s)$ is spatially invariant, we may write

$$g(s,t) = \int_{-\infty}^{\infty} \tilde{G}(s,t; \tau) \tilde{f}(\tau) d\tau \quad (21)$$

where

$$\begin{aligned} \tilde{f}(\tau) &= f(s,t), \text{ and } \tilde{G}(s,t; \tau) \\ &= \int_s G(s,t; \sigma, \tau) d\sigma \end{aligned} \quad (22)$$

We can write equation 21 in differential equation form as

$$\begin{aligned} A_n(s,t) \frac{d^n g(s,t)}{dt^n} + A_{n-1}(s,t) \frac{d^{n-1} g(s,t)}{dt^{n-1}} + \\ \dots + A_0(s,t) g(s,t) = f(s,t) \end{aligned} \quad (23)$$

Usually, we are interested in the output variable at some particular point in space (a particular gaging station), in which case equation 23 becomes

$$A_n(t) \frac{d^n g(t)}{dt^n} + A_{n-1}(t) \frac{d^{n-1} g(t)}{dt^{n-1}} + \dots + A_0(t) g(t) = f(t) \quad (24)$$

which describes a spatially lumped parameter, time-varying linear system. If we assume that the parameters in equation 24 are time invariant, we obtain

$$A_n \frac{d^n g(t)}{dt^n} + A_{n-1} \frac{d^{n-1} g(t)}{dt^{n-1}} + \dots + A_0 g(t) = f(t) \quad (25)$$

which describes a time invariant, lumped parameter linear system. If we assume that the system is completely at rest at $t=0$, we can write equation 25 in the form of the convolution equation

$$g(t) = \int_0^t h(\tau) f(t-\tau) d\tau \quad (26)$$

which is the basis of the unit hydrograph theory and many other hydrologic techniques. In equation 26, $g(t)$ represents runoff, $f(t)$ rainfall, and $h(t)$ is the kernel, or in this case, the unit hydrograph.

In summary, application of equation 26 implies that the watershed behaves as a linear system, it is time invariant, the rainfall is uniformly distributed over the watershed

area, and the watershed is completely at rest at the beginning of the rain. The "effective" precipitation is used as an input to the system. This implies that we know some method for the separation of the runoff hydrograph into base flow and direct runoff (fig. 9). This approach in fact is a combination, using system synthesis for the estimation of the effective precipitation, and system analysis for the estimation of runoff. Methods using this technique have been developed by Snyder (1955), Eagleson et al. (1966), Nash (1957, 1960), O'Donnell (1960), Dooge (1965), and others.

Deterministic Nonlinear Hydrologic Systems

As it was noted in a previous section, a time invariant analytic system can be expanded in Volterra series. Such an expansion can be written in the form

$$\begin{aligned} y(t) = & h_0 + \int_{-\infty}^{\infty} h_1(\tau_1) x(t-\tau_1) d\tau_1 \\ & + \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} h_2(\tau_1, \tau_2) x(t-\tau_1) x(t-\tau_2) d\tau_1 d\tau_2 \\ & + \dots \\ & + \int_{-\infty}^{\infty} \dots \int_{-\infty}^{\infty} h_n(\tau_1 \dots \tau_n) x(t-\tau_1) \dots \\ & \quad x(t-\tau_n) d\tau_1 \dots d\tau_n \\ & + \dots \end{aligned} \quad (27)$$

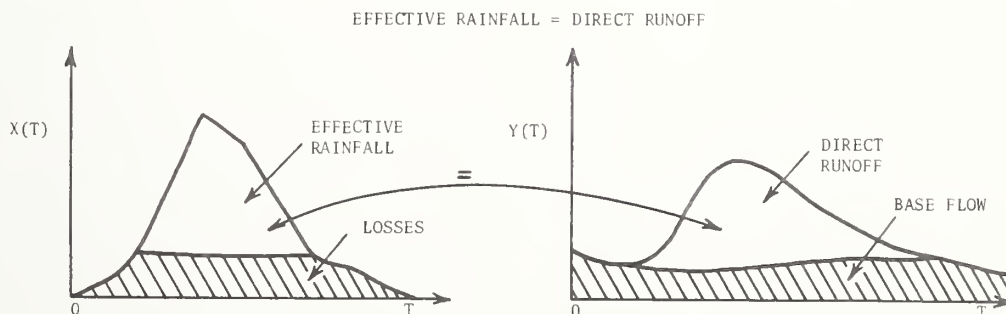


Figure 9. Estimation of effective rainfall through hydrograph separation.

where h_i are the kernels of the system and $h_0=0$ unless a source or sink is present. If the system is physically realizable, and has finite memory (as it happens with hydrologic systems), equation 27 can be written in the form

$$\begin{aligned}
 y(t) = & \int_0^u h_1(\tau_1) x(t-\tau_1) d\tau_1 \\
 & + \int_0^u \int_0^u h_2(\tau_1, \tau_2) x(t-\tau_1) x(t-\tau_2) d\tau_1 d\tau_2 \\
 & + \dots \\
 & + \int_0^u \dots \int_0^u h_n(\tau_1 \dots \tau_n) x(t-\tau_1) \dots \\
 & \quad x(t-\tau_n) d\tau_1 \dots d\tau_n \\
 & + \dots
 \end{aligned} \quad (28)$$

subject to the condition

$$h_i(t) = 0 \text{ for all } \tau < 0$$

and where u is the length of the memory. If, instead of continuous functions, discrete sets of data are used, equation 28 can be written in the form

$$\begin{aligned}
 y(T) = & \sum_{S_1=0}^U H_1(S_1) X(T-S_1) \\
 & + \sum_{S_1=0}^U \sum_{S_2=0}^U H_2(S_1, S_2) X(T-S_1) \\
 & \quad X(T-S_2) \\
 & + \dots \\
 & + \sum_{S_1=0}^U \dots \sum_{S_n=0}^U H_n(S_1 \dots S_n) X(T-S_1) \\
 & \quad \dots X(T-S_n)
 \end{aligned} \quad (29)$$

The first term in equation 28 or 29 represents a linear system, that is an ordinary convolution integral. The other terms are a generalization of the convolution integral. In general, the i th term represents a pure subsystem of order i . Therefore our system $y(t)$ is composed of the summation of a linear and a

series of nonlinear subsystems. If we represent the successive terms of the system by $H_1(t)$, $H_2(t)$, \dots , $H_n(t)$, \dots , respectively, the system can be written in the form

$$y(t) = H_1(t) + H_2(t) + \dots + H_n(t) + \dots \quad (30)$$

An illustration of a nonlinear system is given in figure 10.

A system is identified whenever its kernels $h_n(t)$ are calculated. This evaluation is based on the past behavior of the system. Theoretically, after knowing all the kernels, the response of the system can be calculated for any given set of input values.

Equation 28 (in the form given) is very generalized and its usage is limited and time consuming. It is desirable to reduce the operations involved. For example, given a sequence of inputs, sometimes sequential values are highly correlated, and the system itself may smooth out rapid fluctuations. Hydrologic systems demonstrate both of these characteristics. Thus, we may look for ways which can describe the sequence by a smaller number of parameters. If the sequence $x_1 \dots x_j \dots x_n$ represents observations at times $t_1 \dots t_j \dots t_n$, respectively, they can be approximated by a polynomial of the form

$$X_k(t) = \alpha_0 + \alpha_1 t + \dots + \alpha_k t^k = \sum_{m=0}^k \alpha_m t^m \quad (31)$$

where $k < n$, and such that

$$e_j = |X_k(t_j) - x_j|, \quad (j = 1 \dots n) \quad (32)$$

is sufficiently small. Using such a polynomial approximation a number of difficulties arise. The most important is that the method becomes very sensitive to error when k exceeds 7 or 8 (Forsythe 1957). The use of orthogonal polynomials solves these difficulties. The normal equations of the least square data fitting completely decouple. The evaluation of the standard deviation employing the null hypothesis becomes much less time consuming. Fourier series expansion of a function falls into this category. Another approach is that of weighted polynomial expansion within an interval (the length of memory). If one takes as many polynomials as the length of

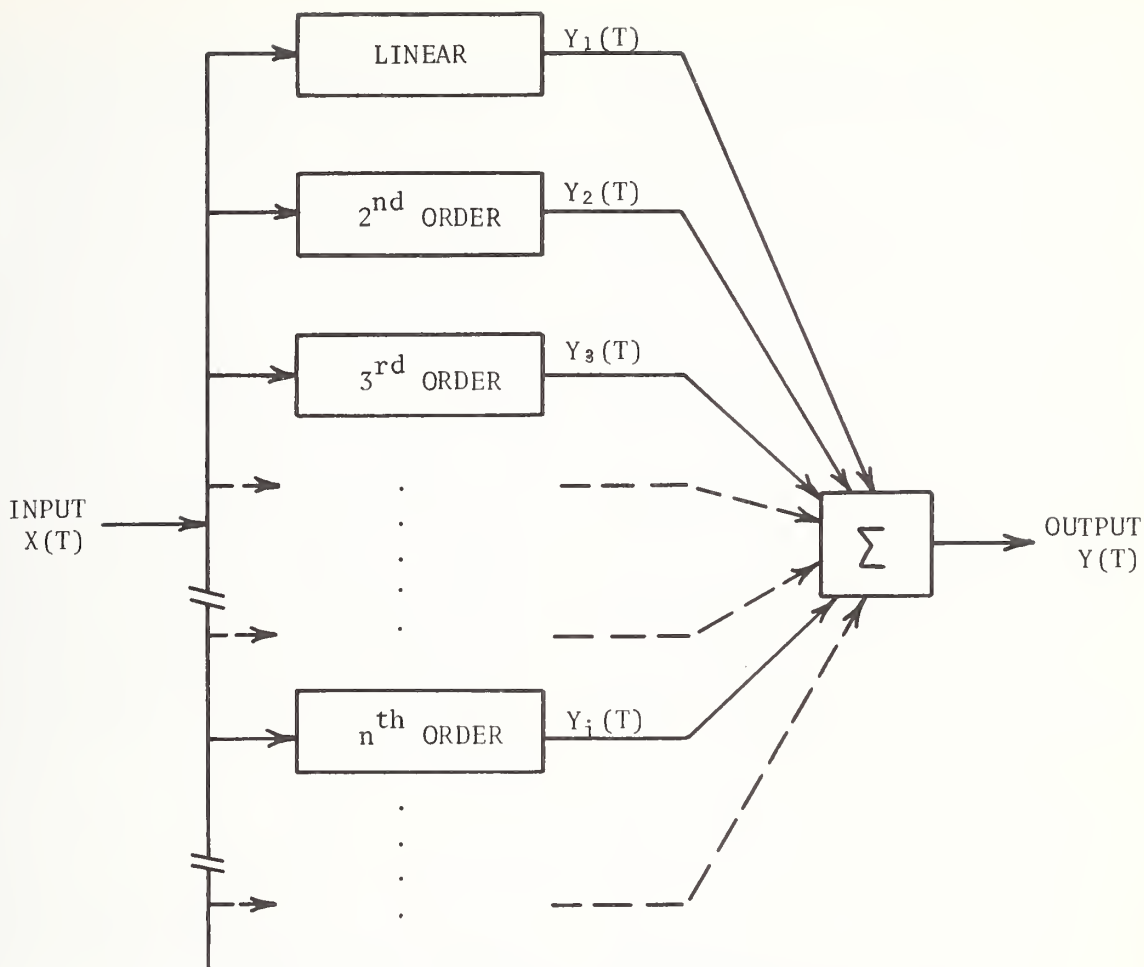


Figure 10. Illustration of nonlinear system representation by Volterra Series.

the memory, an exact match could be made to each of the input values. However, no economy in the description would have been affected. Instead, fewer polynomials can be used. This introduces an error, but due to the nature of the operation, it will be the least error possible.

Methods using the above procedure have been introduced by Jacobi (1966), Harder and Zand (1969), and Brandstetter and Amorocho (1970). It is this method which is being considered for use in this study. There are certain distinct advantages associated with the process. The method is quite general and can handle a variety of problems such as runoff, chemical quality of runoff waters, and suspended sediment predictions, when input values are properly weighted by functions describing the physical processes involved in

each case. Once the response functions or kernels of the system are evaluated, they may be used for predictions given any sequence of inputs. It requires a minimum amount of data, possibly 1 to 2 years of good records. Systems can be used in cascade, like

predict predict
 precip. → runoff → quality or sediment

It can be used for quantitative evaluations of the changes created by any type of watershed management procedure by evaluating the kernels of the original and the managed hydrologic system. Emphasis will be given to establishing weighted functions for the best description of the physical process, and on deriving tools for the greatest economization of the procedure.

Watershed Stratification: A Problem on Watershed 10⁴

We have also begun to structure the hydrologic model for watershed 10 concurrently with the simulation study underway for watershed 2 and the watershed systems analysis. Our objective here is to prepare a fine-resolution hydrologic model which incorporates the transpiration model from the Primary Producers, the evapotranspiration model from Meteorology, and provides soil moisture and subsurface water flow for the Primary Producer and Bio-Geochemical Processes groups. The first step in structuring such a model is system stratification.

One key to the analysis of complex systems is the compartmentalization of the system into homogeneous subsystems which can then

be isolated for study. This should be done in such a way that the linkage between compartments is simple and direct.

Another key is placement of compartment boundaries in such a way that the cells are easily uncoupled, or are coupled as a simple linear cascade. To do otherwise would complicate the modeling considerably. A hydrologic model that consists of a series of compartments arranged as a branching cascade is extremely difficult to manage. Water flow from an upper compartment must be somehow divided between lower compartments in the cascade. The basis for such division is generally obscure and usually arbitrary.

In our attempt to structure the hydrologic model for watershed 10 at the next level of resolution, we began by setting compartment boundaries along stream courses. This automatically decoupled the compartments, since water does not cross the channel (fig. 11).

Next, it was necessary to consider the arrangement of the plant communities within

⁴ Authored by George W. Brown, Associate Professor, Oregon State University, Corvallis.

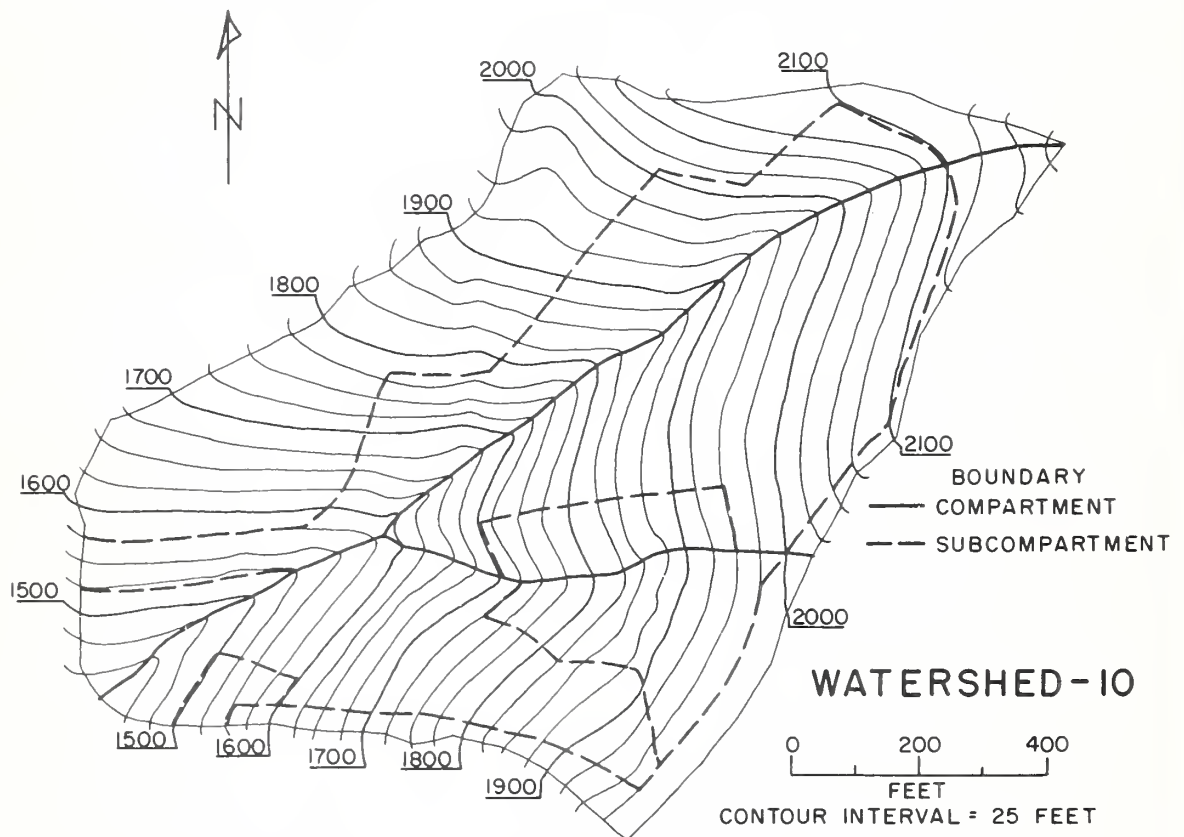


Figure 11. Initial and secondary stratification of watershed 10, H. J. Andrews Experimental Forest, Oregon.

the watershed. The hydrologic model and the primary producer model are obviously linked. The principal coupling variable between models is the soil moisture profile. Soil moisture is that portion of the "hydrologic state" of the watershed which closely regulates plant growth. Plants, in turn, influence soil moisture by transpiration. Thus, superimposition of the primary producer's vegetative structure upon the structure of the hydrologic system is essential. This structure was combined with the initial hydrologic stratification and defined the subcompartment boundaries. Subcompartment boundaries approximate the vegetative type-map boundaries and are arranged into riparian, midslope and ridgetop zones. These zones undoubtedly reflect the changes in soil moisture regime within the watershed. Also, this stratification allows us to consider flow between subcompartments as simple linear cascades.

This final stratification for watershed 10 will provide the basis for sampling schemes to characterize soil moisture, water flow and other hydrologic and biologic processes necessary for the next round of model construction. It is essential to note that this stratification is compatible for modeling hydrologic processes and is also compatible for linking the hydrologic model with that of the primary producers. It is the major achievement of our initial modeling effort and sets the stage for continued progress.

Acknowledgments

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Preliminary considerations of the forest canopy consumer subsystem

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Abstract

A food chain beginning with herbaceous materials produced in the forest canopy is delineated as a subsystem. A conceptual model of energy flow through this subsystem includes assumptions and definitions relating to components of the canopy food chain, processes by which energy is transferred, and the energy pathways. From this conceptual model, it is observed that the canopy food chain is directly coupled to other consumer subsystems through common predators and through the detritus component. Besides the direct relationship through the food base to primary production, this subsystem may also influence the plant system by its effects on the sites of plant hormone production and on the fate of mobile nutrients in the ecosystem.

Introduction

In the past, modeling efforts concerning consumers have been centered on population dynamics, while more recently energetics have been receiving attention. Our considerations of consumers will also concern energy transfer. We will focus on the couplings between consumers and other parts of the ecosystem. These couplings may be direct (i.e., involve energy transfer to or from a consumer) or indirect (i.e., involve the influence of one component on energy transfer between other components of the ecosystem). The major subdivisions of the ecosystem are discussed by Overton (1972).

To facilitate our understanding of the consumer system, it would be convenient to subdivide it into a hierarchical set of units and observe the couplings between them and their couplings with other ecosystem components. If our units are to be subsystems, then the most logical divisions would occur around groups of components with high degrees of interconnections. The majority of linkages with a subsystem's components should occur within the subsystem; couplings to compo-

nents of other subsystems should be comparatively rare. The classic way to define consumer subsystems has been by trophic levels; however, for our purpose this division may not be the most meaningful one. By basing the division of the consumer system on trophic level designations, the direct linkages with regard to energy flow occur between the subsystems and only indirect linkages, such as competition, occur within them. We hypothesize that a better subdivision of the consumer system could be made by defining the subsystems as food chains on the basis of a stratification of their primary food base.

The first division in our hierarchy will be into grazing and detritus food chains. The grazing food chain includes primary consumers feeding on plant material and a series of secondary consumers that prey on the herbivores and on each other. To further subdivide this food chain, the food base is stratified into forest canopy herbaceous material, woody material, forest floor herbaceous material, and roots. Food chains are defined by the food material eaten by the primary consumers in the chain. Likewise, the detritus food chain which recycles detritus to lower

grades of detritus is divided according to particle size. The two resulting food chains use fine or coarse detritus as their primary food sources. By uncoupling these six food chains (four grazing and two detritus) with regard to their food bases, the first order consumers are reasonably unique to a particular food chain subsystem, while common predators couple the subsystems together.

The purposes of this paper will be to define the forest canopy food chain and to develop a conceptual model of it as an example of the type of preliminary consideration which is a prerequisite to mathematical modeling.

The forest canopy food chain forms a subsystem that begins with herbaceous material produced by trees and follows it through its many transfers to detritus. The food base is primarily photosynthetic tissue, needles and leaves of trees; however, buds, young twigs, immature cones, and seeds will also be included, since consumption of these foods is an interrelated process. For present considerations, we will confine our concern to an old-growth, coniferous forest canopy. Successional changes, epidemic outbreaks, and environmental gradients will not be included in our discussions. It is assumed that variations in energy flow from year to year are not appreciable, so there are periods of short-term stability. The conceptual model we will propose is a description of this type of stable condition.

Our discussion will consist of four parts: the components of the subsystem, the processes involved in energy transfer, energy pathways, and the interconnections between this and other food chain subsystems as well as the subsystems defined by Overton (1972) in this symposium. In each section we will present a set of assumptions and definitions that represent our notion of this subsystem. The set will form our conceptual model.

Components

The components of a subsystem are the locations of energy storage and vehicles of energy transfer along the food chain. Components are defined by ecological function

rather than taxonomic criteria. However great species diversity might be in a forest canopy, functional roles are common to many species, enabling them to be regarded as a few large populations. To avoid the pitfall of overgeneralization about the superpopulations, a brief discussion of the variations of behavior relevant to energy transfer of our components is included.

Primary consumers are the key links in the food chains, diverting energy produced by the plants into the animal system. In the forest canopy most consumers are insect grazers which feed mainly on new tissue from expanding needles or leaves (Keen 1952). The feeding stage either hatches or emerges near a feeding site, so that food finding initially is not a problem. Many of them feed gregariously when larvae are small, but disperse to feed singly later. The main dissemination phase, however, is the adult where females seek out new feeding sites for oviposition. The feeding period occurs primarily in the spring and early summer with resting phases (pupae, eggs, or overwintering larvae) beginning in late August or early September. A second group of primary consumers includes insects with sucking mouth parts. They act as physiological sinks and remove dissolved nutrients from the xylem sap (Way and Cammell 1970). Only one significant vertebrate foliage feeder has been reported in the forest canopy—the red tree mouse (*Phenacomys longicaudus*) (Maser 1966). It eats needles of Douglas-fir (*Pseudotsuga menziesii*) leaving the central xylem strand. Small branches are cut and carried to the nest where they are consumed.

Plant reproductive tissues are also consumed. Immature cones are attached mainly by cone and seed feeding insects; some feed exclusively on the seeds, while others feed on the cone preventing seed development. Mature seed may be consumed prior to dissemination by certain birds and squirrels. These omnivorous birds use seeds as a primary food source during the winter; they remove undisseminated seeds while the cones are still attached to the tree (Isaac 1943). Squirrels cut cones and extract the seeds on the ground; the subsequent fate of the seeds is

considered as part of another food chain subsystem which utilizes forest floor herbaceous material.

Predators and parasites constitute the next links in the food chain. Small invertebrates are consumed generally by other invertebrates. Parasitic forms may feed on larvae, pupae, or eggs of the host. Often several generations of parasites are produced for every single host generation; hyperparasitism of several degrees is possible. Predaceous invertebrates include both spiders and insects. Some, as the orb-spinning spiders, wait for mobile forms to be trapped, while others move about actively in search of food and feed on nearly any invertebrate they can capture (Graham 1952).

During the mating and nesting season, omnivorous birds feed on insects with egg hatch often being correlated with peak insect abundance (Lack 1954). Very small larvae are usually not eaten since they are inconspicuous and many would be required to satisfy a bird's energy needs. Flycatchers, which are not abundant in the winter, breed in the forest canopy and feed mainly on adult insects. Other insectivorous birds search the foliage for the larger larvae. Predation of adult birds is rare, but nest predators may be found consuming both eggs and young nestlings. Other predatory birds are also rare components of the forest canopy; however, the spotted owl (*Strix occidentalis*) is an important predator of vertebrate foliage feeders (Nussbaum 1972¹).

The components of the forest canopy food chain are restricted to those animals that can complete at least the feeding stages of their life cycles above the shrub stratum. In our considerations of the forest canopy, we have restricted ourselves to endemic population conditions and have not considered the large numbers of defoliators found in some areas. The actual population densities found under "normal" circumstances is not known for the old-growth stands, and estimates of these densities will be a subject of future research. We will consider herbivores to be predator limited and predators to be food limited. All

components will be assumed to be balanced with respect to immigration and emigration except for seasonally migrating birds.

In summary, we have designated nine superpopulations or components in the forest canopy food chain subsystem: grazing insects, sucking insects, vertebrate foliage feeders, seed and cone insects, omnivorous birds, parasitic invertebrates, predaceous invertebrates, nest predators, and other predatory birds. Energy flow will be followed between these components; possible transfers within them will not be considered explicitly.

Processes

Certain processes are essential for the transfer of energy, and we have defined five main processes for the food chain subsystems: consumption, elimination, respiration, assimilation, and death. The definitions we use may not be the same as those found in ecological literature, but our definitions are consistent with the purpose of defining direct couplings within and between the food chains and other subsystems of the ecosystem.

The concept of consumption is often equated with ingestion; however, the importance of consumers may not be measured by what they ingest alone. Shelter building and wasteful feeding behavior may result in far greater death of the food resource than the amount ingested. Hence consumption will include ingestion as well as other activities of the animals that result in the loss of life of their food. All forms of waste production by animals after the food is ingested is included in the process of elimination. Thus, energy lost as a result of indigestion, metabolic wastes, or losses of integument will be transferred to detritus via elimination. Assimilation is defined as individual secondary production. It is the process by which energy from one trophic level is incorporated into the tissue of the next. The process of respiration includes the energy loss to the atmospheric sink as the result of maintenance metabolism and of work. Death includes mortality losses as a result of factors other than consumption by another component of a food chain. Both the

¹ Personal communication.

processes of death and elimination result in the production of detritus, but they must be considered separately since they differ in their consequences to the food chain components. Elimination does not affect the potential activity of a component, whereas, death may.

The purpose of defining these five processes is to identify the means by which components are directly coupled with each other or with other subsystems of the ecosystem. Each one is influenced by indirect couplings. For example, feeding behavior, population age structure, and energy demands are indirect couplings between the feeding population and the process of consumption. Nutritional quality of the food may influence the processes of assimilation and elimination. These indirect couplings may be thought of as informational transfers and may be as impor-

tant to the system as the direct couplings.

Energy Pathways

The general energy pathway is diagrammed in figure 1. The boxes are used to show sites of energy storage. They are associated with a set of variables which are used to describe the site. The consumed tissue compartment is a hypothetical site but is included to separate the processes of consumption and assimilation. Circles are used to indicate the processes which are employed to transfer energy between sites. Solid arrows mean true flows of materials or energy (direct couplings), while dotted arrows and diamonds indicate lines of influence (indirect couplings) from an energy storage site to a process.

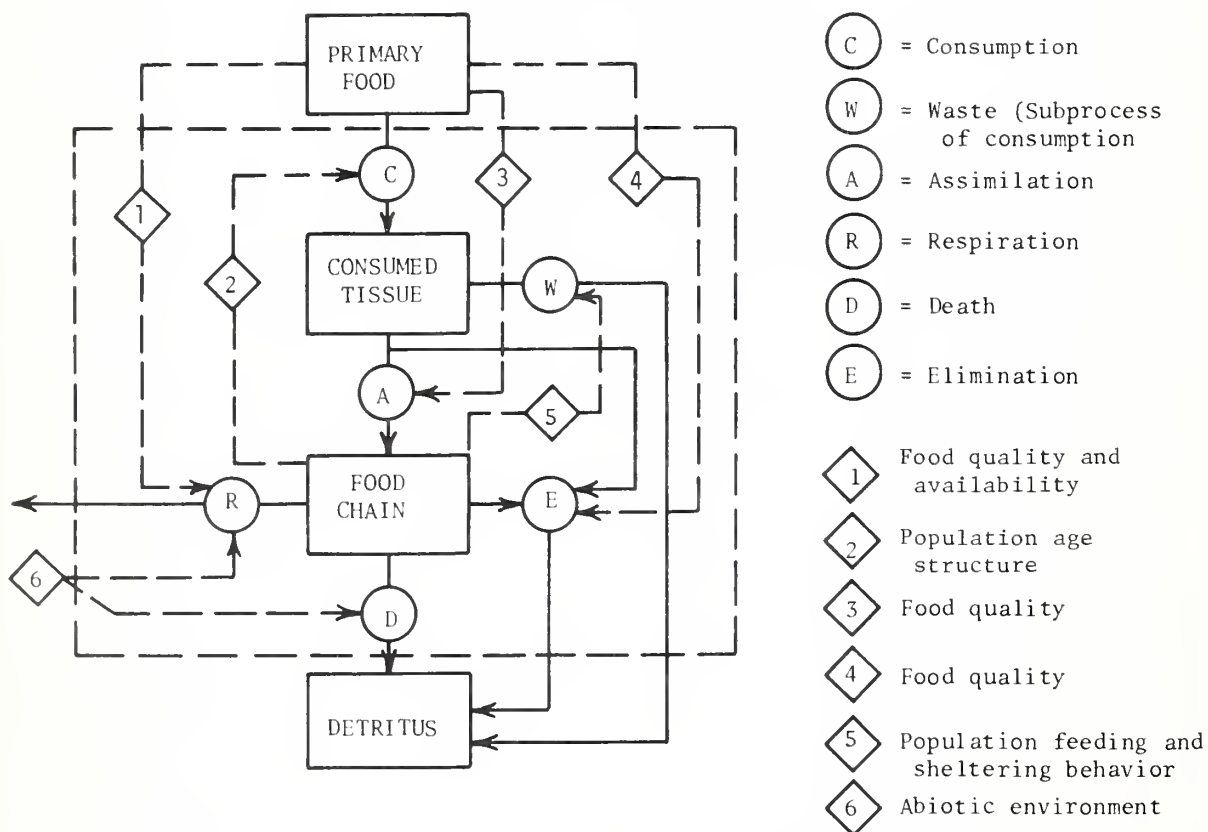


Figure 1. Basic energy pathway through food chain subsystem. See text for explanation of symbols.

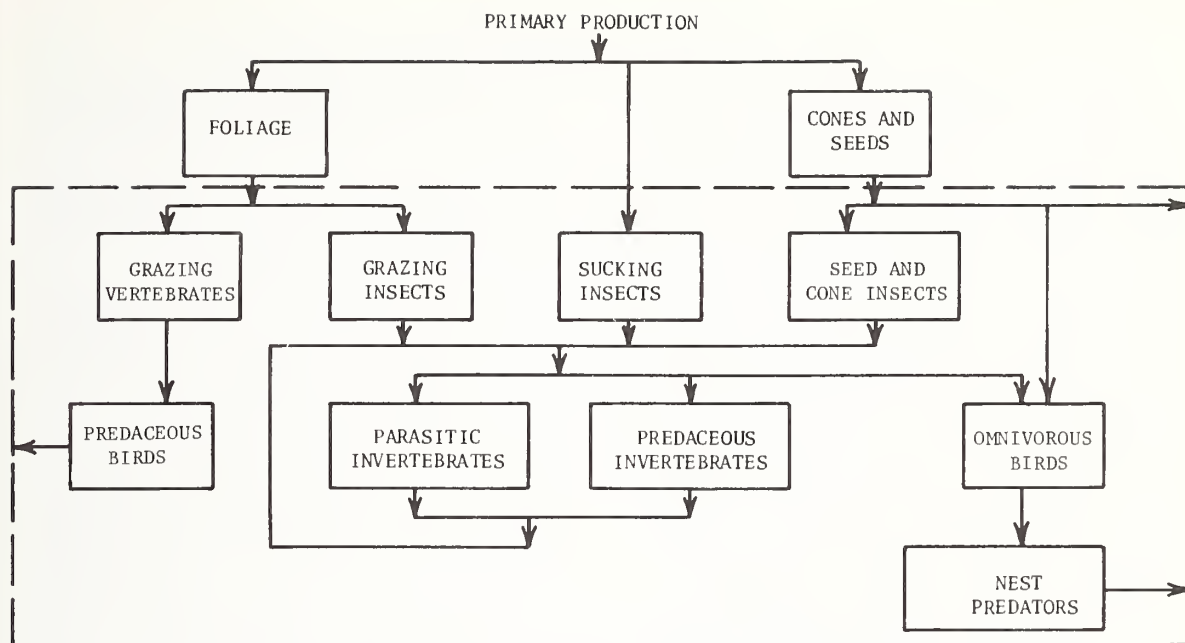


Figure 2. The major energy pathways between components of the forest canopy food chain.

The paths of energy (fig. 2) may be followed beginning in the spring when the buds of the conifers swell and insect herbivores emerge and feed. While they are small, the grazing and sucking insects are preyed upon by other invertebrates. Later they are preyed upon by birds that switch from conifer seeds to insect larvae during their breeding season. Energy leaves the system in the form of food for predators in other food chains, migrating birds, detritus, and heat. The amounts of energy following these routes is not known yet. Consumption rates, relative densities of consumers, food quality variability, assimilation efficiencies, and migration habits are also not known for most of the consumers. These problems will require further research before the model may be quantified. The two diagrams and the definitions and assumptions that were outlined in the preceding sections represent our current conceptual model of the canopy food chain.

Interconnections with Other Subsystems

The conceptual model presented here of the forest canopy consumer subsystem may be used to describe possible interrelations between it and other subsystems. By definition, this subsystem contains consumers that feed primarily in the forest canopy; therefore, we would not expect it to be tightly coupled to other food chains. However, since the food base defines the subsystem and, in the case of the canopy food chain, herbivores are more specific in food habits than the carnivores, it is evident that direct couplings will probably result from the feeding behavior of the secondary consumers. For example, adult insects from other subsystems may serve as food for flycatcher birds which live primarily in the canopy. Predaceous invertebrates from the forest floor feed upon canopy species

when they move to the floor for overwintering or pupation. The food chain with primary consumers that feed on fine detritus is coupled to this subsystem through the detritus output, and the canopy food chain may influence the energy flow rates within the detritus food chain by the quality of its detrital outputs.

Besides these connections with other food chain subsystems, the canopy consumers are closely linked to the primary production system. The consumers are influenced by the quantity and quality of herbaceous material produced by the trees. However, the influence of the canopy food chain on primary production is more subtle. Although consumption of foliage or cones is not considered to be at a rate to affect production in the old-growth canopy of the model, the preferential consumption of new needles and expanding cones may affect the nutrient capital of the trees. These consumption sites are physiological sinks, and mobile nutrients are actively moved to them from senescent foliage and storage sites (Sweet and Wareing 1966). The loss of these sinks may mean the return of certain nutrients to the soil solution rather than their retention by the trees (Rafes 1970). Also, consumption of bud tips reduces the sites of growth hormone production; this hormone is necessary for cambial division, and local deficiencies may result from the gregarious feeding habits of some herbivores (Kozlowski 1969). These indirect couplings may prove to be the most significant role of the food chain subsystems in the old-growth forest.

Summary

The consumer system is composed of a series of grazing and detritus food chains. The primary consumers are thought to be reason-

ably unique to each food chain, and direct energy transfers between the food chains occur via common predators. The processes of energy transfer that link the components of the food chains with each other and the rest of the ecosystem are: consumption, assimilation, elimination, respiration, and death. Indirect links are formed by informational transfers which influence energy flows.

The forest canopy food chain includes the primary consumers that feed on herbaceous material produced in the canopy and the series of related predators. This food chain is directly linked to primary production by consumption of herbaceous materials, to the other food chains by common predators, and to the detritus component through production of detrital material. Primary production influences the food chain processes by variations in nutritional quality, spatial arrangement, and quantity of material produced. The influences of the food chain on primary production are more subtle. Preferential feeding habits of many canopy grazers affect the number of sites of plant hormone production and the fate of mobile nutrients in the ecosystem.

Acknowledgments

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An environmental grid for classifying coniferous forest ecosystems

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Abstract

To develop models which will predict primary production and forest composition across the Biome, we suggest that the environment be defined operationally as it affects certain plant responses. Models can be developed which indicate how water, nutrients, light, temperature, and mechanical factors interact through the plant to control primary production and plant composition. Plant responses including water stress, stomatal behavior, foliar nutrition, and phenology, among others, were coupled to environmental variables to create plant response indices for soil moisture, temperature, transpiration, and soil fertility. By correlating indicator species with plant response indices, an ecosystem can be defined environmentally without direct measurements. Other processes including biogeochemical cycling, consumer population dynamics, and hydrologic functions may also be related to the environmental grid.

Introduction

Diversity in environment and vegetation is characteristic of the Coniferous Forest Biome. Such diversity is esthetically pleasing but presents formidable problems of classification. Classification is necessary, however, if we are to understand the processes which affect the composition and allow for continued productivity of the forests and related water, wildlife, and recreational resources.

If we could understand how the environment influences forest growth and composition, we would be well on the way toward reassessing our past management successes and failures. We could also make our detailed ecosystem studies more widely applicable in both time and space, thus providing a framework for intelligent land management. The problem lies (a) in identifying which properties of the environment should be measured, (b) coupling these to important biological

processes, and (c) finally in predicting certain key properties of ecosystems.

In this paper we attempt to establish a conceptual basis for evaluating environment, then test the general approach, and finally suggest necessary modifications to permit extension across the Coniferous Forest Biome.

General Theory

The Operational Environment

Excellent descriptions of vegetation and regional physiography exist for many regions of the world. In the Pacific Northwest the most thorough treatments have been provided by Daubenmire (1952), Krajina (1965), and Franklin and Dyrness (1969). Detailed physiographic classification such as that developed by Hills (1959) has proven most use-

ful in regions with relatively uniform climate.

Probably the most helpful classifications from a standpoint of predicting the nature of forest ecosystems, however, have been those related to environmental gradients (Warming 1909, Sukachev 1928, Pogrebnjak 1929, Bakuzis 1961, Ellenberg 1950, 1956, Rowe 1956, Whittaker 1956, 1960, Loucks 1962, Waring and Major 1964). Unfortunately, all previously defined environmental gradients cannot be directly applied outside the particular region where they were developed. We feel environmental gradients can be more widely utilized only when the environment is coupled to basic processes controlling plant growth and composition. We believe a key to expanding the gradient analysis approach is to focus more closely upon the basic physiological behavior of plants.

Fortunately a foundation for a process-oriented approach has already been laid. Mason and Langenheim (1957) defined the idea of an "operational environment" as one which directly affects an organism. Implicit in their concept of environment is the recognition of specific plant responses to environmental stimuli. In fact, these authors felt that "environment" could not exist independently in an ecological sense. It must have an effect upon an organism. Although they did not define measurable environmental stimuli, their very definition of an "operational environment" focuses attention upon the influence rather than on the origin of the stimulus.

Thus, in an interpretive ecological sense, it is more important to assess the availability of water to plant roots than the origin of that water. This distinction greatly reduces the number of factors requiring consideration, for although altitude, slope, and other physiographic features are correlated with vegetation, such indirectly operating factors may be ignored if the mode of action can be identified and measured. Ellenberg (1956), Bakuzis (1961), Waring and Major (1964), and others have suggested that vegetation responds to changes in water, temperature, light, and chemical and mechanical factors. Although these factors do not operate independently, they cannot completely substitute for one another.

General Approach

We still have to translate the concept of an "operational environment" into a design adequate for research. As a first step we can diagram the flow of material through a plant into various compartments and identify the controls on the rate of flow imposed by the environment, the organism, or the amount of material in a given compartment. Figure 1

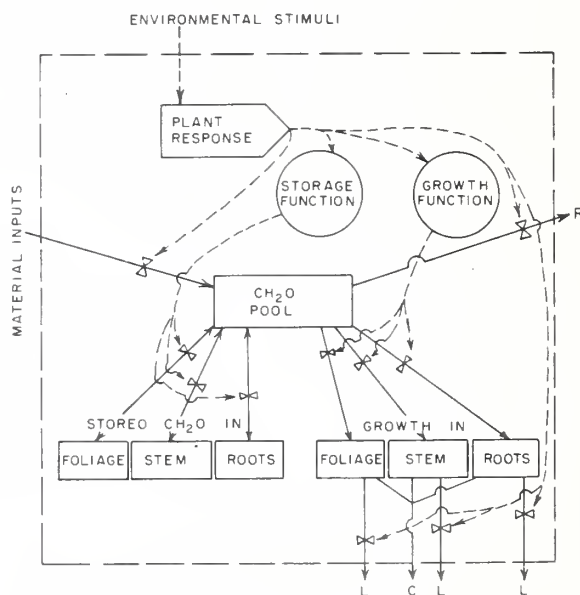


Figure 1. General model of primary production. Material inputs of H_2O , CO_2 , and energy flow into the system to form carbohydrates. The rate of incorporation (photosynthesis) is a function of various plant responses. These responses are triggered by a host of environmental stimuli: temperature, light, humidity, soil water potential, soil fertility, and mechanical stress. The plant responses interact to provide two functions: (1) a control on carbohydrate storage and (2) a control on growth. Losses from the system are through respiration (R), death of roots and other organs and in litter (L), and consumption by animals (C).

presents such a diagrammatic model. The rectangles are the compartments, and the flow of materials is indicated by solid lines, while dotted lines indicate the transfer of information through valves controlling the rate of material flow from one compartment to an-

other. The plant integrates environmental stimuli. Arrows indicate the direction of flow, and circles are special functions regulated by information from the plant integrator.

We interpret environmental variables as being external to the system and impinging upon it. The system, in this case the organism, responds only in accordance to the external stimuli. Modifications in the environment brought about by the organism itself are not distinguished from those originating through other means.

The amount of material transfer from environment to plant is determined by the kind and magnitude of the response; i.e., the amount of CO_2 converted into carbohydrate is determined by the photosynthetic rate. The amount of carbohydrate utilized in the growth of foliage, stem, and roots is also affected by the stage of plant development and other plant responses. As long as the carbohydrate pool does not become exhausted, or one of the plant responses is not death,

biomass can accumulate.

When the environment initiates a lethal plant response, the transfer of carbohydrates is stopped and all of the biomass compartments empty. Biomass loss also occurs through respiration, consumption by animals, the normal fall of litter, and death of roots and twigs.

Unfortunately, we do not, at present, have adequate knowledge for complete evaluation of such an energy flow model, even for a single species. We hope to acquire much needed data through the Biome program. Still it is safe to say that we will lack complete data on most species to predict accurately the system's response to external variables. Our approach, therefore, is to study physiological responses in relation to the environment, develop functional models, and from these create plant response indices as a means of interpreting environmental gradients. Further, we propose to correlate ecosystem properties with these plant response indices. Figure 2

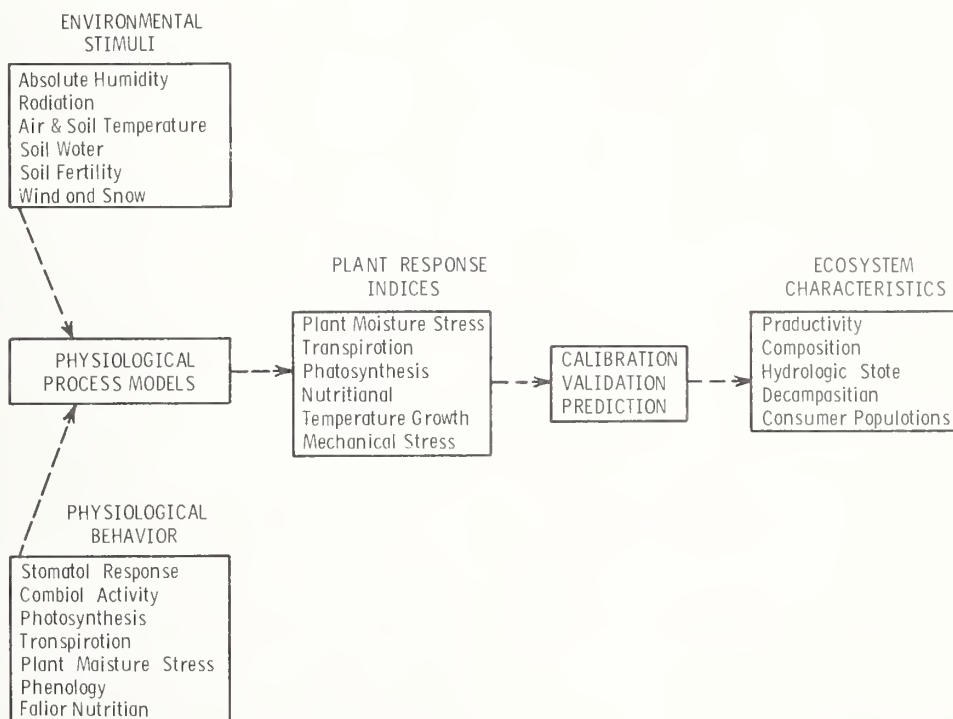


Figure 2. Physiological process models couple environmental stimuli to the physiological behavior of selected conifers. From an understanding of the process models, plant response indices are derived which reflect major environmental gradients. These indices locate ecosystems within an environmental grid and through correlation permit certain ecosystem characteristics to be predicted.

represents the basic linkages between environmental stimuli, physiological behavior, and the generation of plant response indices which are to be correlated with ecosystem characteristics.

The Organism

If we strive for both a predictive model and an understanding of the general processes controlling plant composition, we must compromise by linking observations of plant distribution and growth for many species to the physiological behavior of certain trees. For in this Biome, trees represent the dominant form in which energy accumulates in forest ecosystems.

The size of reference plants must also be standardized. Although establishment is critical for determining the composition of any plant community, young seedlings represent both adapted and ill-adapted plants. Mature plants, on the other hand, are usually so well established that their responses only hint at the critical selective factors operating at the time of establishment and early growth. As a compromise, in this Biome we study recently established conifers between 1-2 m tall. Few such trees will die during the course of measurements; yet they are small enough to reflect the major environmental forces acting at the critical time of establishment.

Having decided upon the important environmental factors and the size and kind of reference plant, we are still faced with coupling the environment to plant responses. The most commonly selected response has been growth in some form or another, but growth reflects the total integration of all environmental influences and a host of different environmental combinations can result in similar productivity. We choose responses related to the entire plant, but those which may be more closely identified with specific environmental stimuli.

Physiological Behavior

Because plants are a complex system, no response is completely unrelated to another. Therefore most responses cannot be inter-

preted without knowledge of others, and cause and effect relationships can rarely be implied. The most important behavior includes:

1. **Phenological development.** This reflects past environment and serves to define periods during which the sensitivity of the plant is similar. Lack of attention to phenological development is a major reason why otherwise good environmental data are often difficult to interpret ecologically (Azzi 1955).
2. **Carbon dioxide exchange** provides a ready means of quantifying the effects of light and temperature upon photosynthesis.
3. **Plant moisture stress** (plant water potential) before dawn is an excellent measure of how a reference plant responds to soil water status.
4. **Stomatal resistance** reflects the influence of evaporative stress and soil drought, as well as certain other environmental variables.
5. **Foliar nutrition** indicates the interaction between supply of nutrients in the soil and the demand for nutrients.

Results of Past Studies

To help clarify the above discussion, we draw upon our experience during the last 8 years in an environmentally and floristically diverse region of southwestern Oregon (Whittaker 1960, 1961; Waring 1969).

At all or some of the 25 forest stands described briefly in table 1, environmental data on air and soil temperature, radiation, humidity, soil moisture, and soil fertility were recorded. Physiological response studies on two widely distributed conifers, Douglas-fir (*Pseudotsuga menziesii*) and Shasta red fir (*Abies magnifica* var. *shastensis*), included observations of phenology, plant water potential, stomatal resistance, and foliar nutrition. Productivity was estimated by measuring terminal elongation or total height of dominant old-growth trees. Details of this work have been published elsewhere (Waring and Cleary 1967, Waring 1969, Atzet and Waring 1970,

Table 1.—Description of stands

Stand	Elevation	Slope	Aspect	Parent material	Dominant vegetation
	<i>Meters</i>	<i>Percent</i>			
3	780	45	N	Granite	Douglas-fir, black oak, ponderosa pine
21	550	75	N	Metavolcanic	Douglas-fir, black oak, Oregon white oak
8	1,280	40	SW	Granite	Ponderosa pine, Douglas-fir
12	1,585	70	WSW	Green schist	Ponderosa pine, Douglas-fir
1	1,490	25	W	Granite	White fir, ponderosa pine, Douglas-fir
11	1,370	35	SW	Granite	Ponderosa pine, sugar pine, white fir, Douglas-fir
13	1,340	20	W	Green schist	Douglas-fir, ponderosa pine, sugar pine, white fir
19	1,250	70	W	Mica schist	Douglas-fir, sugar pine, white fir
2	1,675	60	WNW	Granite	White fir, Douglas-fir
9	1,550	55	NNW	Metavolcanic	White fir, sugar pine, Shasta red fir
14	1,585	45	E	Green schist	Douglas-fir, white fir
22	1,460	50	N	Metasedimentary	Douglas-fir, white fir
7	1,920	20	N	Granite	Shasta red fir
16	1,890	40	SW	Mica schist	Shasta red fir
17	1,830	10	E	Metavolcanic	Shasta red fir
6	2,040	35	NNE	Granite	Mountain hemlock, Shasta red fir
15	2,010	10	NE	Mica schist	Mountain hemlock
18	2,135	30	NE	Granite	Mountain hemlock
24	2,040	45	NNE	Metavolcanic	Mountain hemlock
4	1,920	65	SE	Ultrabasic	Jeffrey pine, incense-cedar, western white pine
5	1,710	65	SE	Ultrabasic	Jeffrey pine, incense-cedar
25	1,740	5	SE	Ultrabasic	Jeffrey pine, white fir, incense-cedar, Douglas-fir
20	760	70	NNW	Mica schist	Douglas-fir, Pacific yew
23	1,400	10	N	Granite	Engelmann spruce, Douglas-fir, white fir
10	1,740	55	N	Metavolcanic	Brewer spruce, Shasta red fir, mountain hemlock

Cleary and Waring 1969, Reed 1971, Emmingham 1971, Waring and Youngberg 1972). In this article we will restrict discussion to interpretation of results, concentrating upon the operational effects of water, temperature, and soil fertility. Mechanical stress from snow creep or ice storms was important as was wind (Tranquillini 1970), but such adverse mechanical forces are closely associated with temperature gradient. Light, too, was important in understanding succession and accounted for more than 75 percent of the variation in terminal elongation of *Abies* when other environmental factors were restricted to narrow ranges (Emmingham 1971). In our stands, which were mature forests, maximum height of mature trees was used as an index to productivity. In such a situation, earlier reductions in growth due to shading or mechanical damage could be ignored.

Measurement and Interpretation of Plant Water Stress

During the growing season, plant moisture stress measured by the Scholander pressure chamber (Scholander et al. 1965, Waring and Cleary 1967, Boyer 1967) provided a good estimate of plant water potential (Waggoner and Turner 1971). We took measurements at monthly intervals, with more frequency during September when the vegetation was under the greatest stress.

Plant moisture stress usually increases from a predawn minimum to some maximum level in the afternoon. Predawn stress represents the nearest equilibrium between soil and plant water potential. Not only the diurnal pattern but also the seasonal changes in plant water stress are important. The first reflects an imbalance between transpiration and water uptake; the latter can be related to the availability of soil water over a season. In figure 3, three contrasting forest types are shown to have different seasonal water stress curves. The type dominated by Engelmann spruce (*Picea engelmannii*) was restricted to moist sites, while oak (*Quercus kelloggii*) grew where stress was sufficient to bring about cessation of cambial activity in the reference

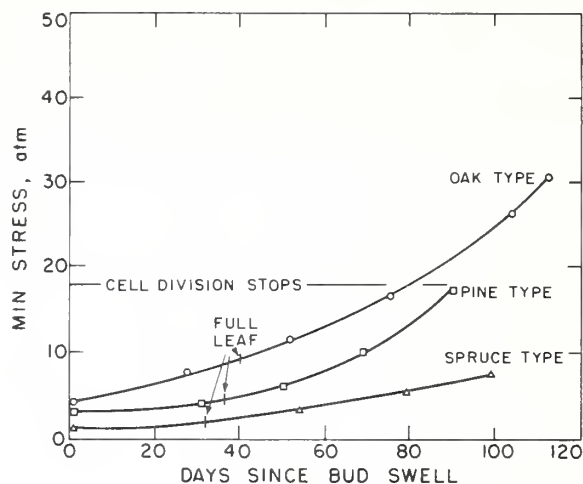


Figure 3. Seasonal changes in minimum plant moisture stress associated with different forest eco-systems (Waring 1970). All data are from 1- to 2-m-tall Douglas-fir. For this particular set of data, the end of season Plant Moisture Stress Index would be 30 for the Oak Type, 18 for the Pine Type, and 7 for the Spruce Type.

plants. Where no rainfall occurs during the summer, the minimum night moisture stress at the end of the growing season is an index to the plant moisture conditions throughout the entire season. From figure 3, we see the oak type had a plant moisture stress index of 30; the pine, an index of around 18; and the spruce, 7 atmospheres. Where summer precipitation is important, a mathematical description of the seasonal trend is desirable (Reed 1971). Winter drought due to cold or frozen soils should also be similarly evaluated.

Measurement and Interpretation of Temperature

At each of the 25 forest stands, air temperature and soil temperature were recorded on 30-day thermographs because both root and shoot temperatures are important. At the time, we did not have photosynthetic response information to help interpret the effect of various combinations of temperature and light. Because winter temperatures are often below freezing, winter photosynthetic activity is probably less in the study region than in the milder climate along the Pacific

coast. Without the benefit of good photosynthetic data, we used laboratory studies conducted by our colleague, D. P. Lavender. Lavender found that the dry weight increase of Douglas-fir seedlings was closely related to both air and soil temperatures. With these data a temperature-plant index was developed by summing the potential growth possible for each day during the growing season (Cleary and Waring 1969). Other variables were assumed nonlimiting. In the field, the Temperature Growth Index ranged from 30 near timberline to nearly 100 on oak and pine forests. Douglas-fir was not found where the index was below 40.

To visualize this information more effectively, the distributions of selected conifers are presented in relation to these two rather simple plant response indices (fig. 4). The distributional patterns closely reflect the adapta-

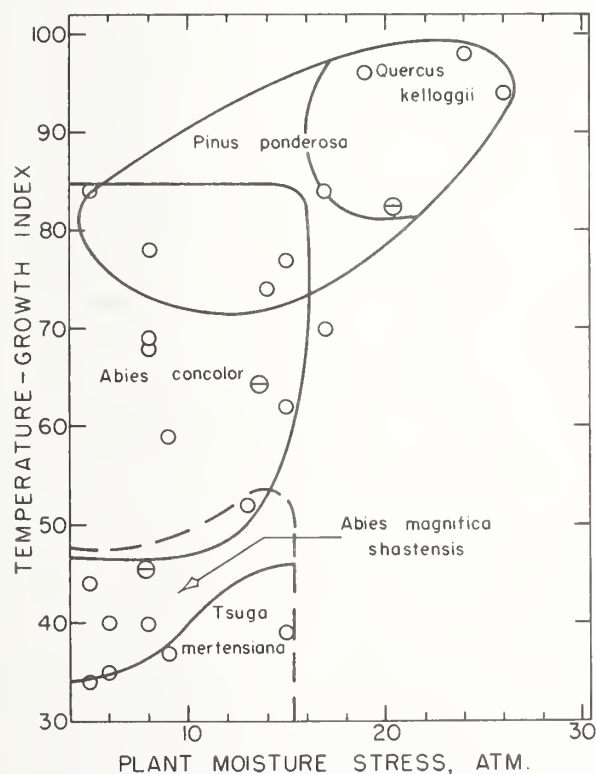


Figure 4. Distribution of natural regeneration in relation to gradients of moisture and temperature defined by plant response indices (Waring 1970). Validation stands, symbolized by \odot , had vegetation predicted by the intercept of their plant response indices.

tion of the various conifers. In a local region, the variation in distribution of different species provides a means of predicting the environment through association with measurements taken on reference plants. The plant response indices were correctly predicted from knowledge of plant distributions for three validation stands, indicated as divided circles in figure 4. It is significant that such predictions are possible without physiological observations on species other than the reference plants and without special attention to events controlling establishment. Once such relationships are established, the vegetation can provide understanding of the operational environment without requiring additional measurements of any kind. We shall expand this idea later.

Measurement and Interpretation of Stomatal Response

Conifer stomata are most difficult to observe, usually being sunken and occluded by wax. The resistance which they offer to the transfer of water vapor from the interior of the needles can be assessed by determining the rate of water vapor movement with a diffusion porometer (Waggoner and Turner 1971). The aperture of stomata may be estimated by observing the pressure necessary to force a 50-percent ethanol solution through the pores (Fry and Walker 1967). The diffusion resistance is then determined by calibrating these pressures with reduction in transpiration under known vapor pressure gradients (Reed 1971). The latter procedure was followed in our past fieldwork. We found that stomatal resistance increased as the soil moisture became less available during the growing season. Further increase in stomatal resistance was possible during the day if evaporative stress was high. These relationships were quantified and developed into a simulation model by Reed (1971). With knowledge of temperature, humidity, and nocturnal plant water stress, the model predicted on a daily basis, both potential transpiration (PT) and transpiration (T) with stomatal control. These values were summed for the entire season and confirmed the obser-

vation that species such as Brewer spruce (*Picea breweriana*), Port-Orford-cedar (*Chamaecyparis lawsoniana*), vine maple (*Acer circinatum*), and rhododendron (*Rhododendron macrophyllum*) are restricted to areas with low potential transpiration. The most valuable index, however, was the ratio of actual to potential transpiration (T/PT) which integrates for water, the demand, the supply, and the control by the plant. Where soil moisture was never inadequate and the evaporative stress remained low, the ratio was 1.0. Where water became limiting and high evaporative stress was common, ratios of 0.3 were calculated. Under these conditions, both forest composition and growth were dramatically affected.

Measurement and Interpretation of Soil Fertility and Plant Nutrition

Soil profiles from each stand were reconstructed to a depth of 60 cm and taken into controlled environment chambers where seedlings of Douglas-fir and Shasta red fir were grown for a period of 5 months (Waring and Youngberg 1972). The dry weight yields at the end of the experiment were used as a bioassay of soil fertility, representing the supply of nutrients available to conifers. Foliar analyses were made on reference trees, first during the time of maximum demand when new foliage was being produced and again after all shoot and diameter growth had ceased in the fall. In the first period, 1-year-old foliage was assessed because it represents a major source of mobile nitrogen, phosphorus, and potassium. Three categories of nutrient availability can be identified: (1) where no nutritional stress occurs during the year; (2) where nutrition is adequate only when shoot and diameter growth has ceased; and (3) where nutrition is inadequate year around (Waring and Youngberg 1972). These three categories may be further refined and are of considerable value in reaching decisions concerning fertilization. The composition of vegetation is, however, insensitive to this classification of nutrient availability.

Only on soils where an imbalance of nutrients or toxic amounts of certain heavy metals

were present did special plant communities develop. In this paper, therefore, we have assigned plants to one of three categories of tolerance to infertile soils developed from ultrabasic parent materials: In class 1 are those which are tolerant; class 2 is made up of those species that are intolerant; and in class 3 are those plants both tolerant and competitively restricted to ultrabasic soils.

Vegetation as an Index to Environment

Can we use plants to define their environment, or more precisely, the environment expressed through reference plants? To test this idea, we selected 47 species from more than 600 in the local flora and recorded their distributional limits in relation to various environmental plant indices (table 2). For some plants we knew only the approximate ranges and occasionally we had insufficient data to set particular index limits.

In forest ecosystems where plant composition is known, the range of environmental indices may be predicted from information in table 2. In table 3, the plant response indices were thus predicted for the 25 stands described in table 1. Therefore for the black oak forest, stand 3, where *Rhus diversiloba*, *Arbutus menziesii*, *Lonicera hispidula*, and *Quercus chrysolepis* grew, one can assess from table 2 that the Temperature Growth Index lies between 98 and 96, the Plant Moisture Stress Index at 25.4, and the ratio of transpiration to potential transpiration as 0.29.

Plants that were exclusively adapted to ultrabasic soils, such as Jeffrey pine, isolated those ecosystems (stands 4, 5, and 25). Those forests with oak (stands 3, 8, and 21) exhibited the greatest water stress, the warmest environments, and the greatest control of transpiration. At the other extreme, mountain hemlock forests (stands 6, 18, 15, and 24) had the coolest environments and lowest potential transpiration.

In figure 5, the midpoint of the predicted Temperature Growth Index from table 3 is plotted against the Temperature Growth Index calculated from temperature records. The regression has an r^2 of 0.93, and is highly

Table 2.—Ecological distribution of selected species in relation to plant response indices¹

Generic name	PT, maximum	PT, minimum	T/PT, maximum	T/PT, minimum	PMS, maximum	PMS, minimum	TGI, maximum	TGI, minimum	Soil tolerance
ANACARDIACEAE									
<i>Rhus diversiloba</i>	30.0	17.7	0.42	0.29	25.4	20.3	100	80	1
BERBERIDACEAE									
<i>Achlys triphylla</i>	16.8	—	1.00	.57	16.2	—	80	60	2
CAPRIFOLIACEAE									
<i>Lonicera hispidula</i>	30.0	17.7	.29	—	30.0	25.4	100	95	1
COMPOSITAE									
<i>Arnica latifolia</i>	13.5	7.5	1.00	.46	19.1	5.2	75	35	2
CUPRESSACEAE									
<i>Libocedrus decurrens</i>	19.5	12.2	1.00	.40	30.0	5.2	85	52	1
ERICACEAE									
<i>Arbutus menziesii</i>	30.0	—	1.00	.29	30.0	5.2	98	68	1
<i>Arctostaphylos viscida</i>	30.0	17.7	.42	.29	25.4	20.3	100	90	1
<i>Rhododendron macrophyllum</i>	12.5	—	1.00	.57	16.2	—	100	—	2
<i>Vaccinium membranaceum</i>	12.5	—	.63	.46	19.1	12.8	60	45	2
<i>Vaccinium scoparium</i>	10.3	—	1.00	.46	19.1	—	50	—	2
FAGACEAE									
<i>Castanopsis chrysophylla</i>	19.5	—	1.00	.51	15.3	—	85	40	1
<i>Quercus chrysolepis</i>	30.0	12.0	1.00	.63	30.0	8.0	100	78	1
<i>Quercus kelloggii</i>	30.0	17.6	.42	.29	30.0	15.0	98	80	1
<i>Quercus sadleriana</i>	16.8	—	1.00	.46	19.1	—	70	50	1
<i>Quercus vaccinifolia</i>	30.0	—	.40	—	30.0	—	100	—	1
GARRYACEAE									
<i>Garrya fremontii</i>	30.0	12.7	.62	.40	30.0	12.6	70	50	1
LABIATAE									
<i>Monardella odoratissima</i>	21.4	—	.62	.40	20.3	12.6	100	35	1
LEGUMINOSAE									
<i>Lathyrus polyphyllus</i>	13.1	—	1.00	.63	12.8	5.2	85	45	2
<i>Lupinus leucophyllus</i>	30.0	12.7	.86	—	30.0	8.4	70	50	3
LILIACEAE									
<i>Clintonia uniflora</i>	13.1	7.5	1.00	.51	16.2	5.2	85	35	2
<i>Disporum hookeri</i>	16.8	12.2	1.00	.51	16.2	5.2	85	45	2
<i>Xerophyllum tenax</i>	19.5	—	1.00	.40	19.1	8.4	80	40	1
PINACEAE									
<i>Abies concolor</i>	19.5	—	1.00	.46	19.1	5.2	84	47	1
<i>Abies magnifica</i> var. <i>shastensis</i>	12.5	7.5	1.00	.46	19.1	5.2	59	34	2
<i>Picea breweriana</i>	10.3	—	1.00	.46	19.1	—	52	—	1
<i>Picea engelmannii</i>	11.0	—	1.00	.63	12.8	—	47	—	2
<i>Pinus jeffreyi</i>	25.0	12.7	.61	—	25.0	8.4	100	52	3
<i>Pinus lambertiana</i>	21.4	11.0	1.00	.29	25.4	5.2	96	45	1
<i>Pinus ponderosa</i>	21.4	13.5	1.00	.29	25.4	5.2	98	68	2
<i>Pinus monticola</i>	19.5	7.8	1.00	.46	19.1	5.2	70	44	1
<i>Pseudotsuga menziesii</i>	21.4	—	1.00	.29	25.4	5.2	98	47	1
<i>Tsuga mertensiana</i>	11.0	7.5	1.00	.46	19.1	5.2	59	34	2
POLEMONIACEAE									
<i>Phlox adsurgens</i>	16.8	10.3	1.00	.46	19.1	5.2	85	52	2
<i>Polemonium californicum</i>	7.8	—	1.00	.98	5.2	—	50	30	2
POLYGONACEAE									
<i>Polygonum davisiae</i>	7.8	—	1.00	.98	5.2	—	40	30	2
POLYPODIACEAE									
<i>Onychium densum</i>	30.0	12.7	.62	—	18.1	5.2	80	50	3
RANUNCULACEAE									
<i>Anemone deltoidea</i>	19.5	7.8	1.00	.51	19.1	5.2	85	45	1
<i>Anemone lyallii</i>	19.5	7.8	1.00	.51	15.3	5.2	75	45	2
ROSACEAE									
<i>Amelanchier pallida</i>	16.8	—	.62	.46	19.1	—	75	50	1
<i>Rubus lasiococcus</i>	12.5	—	1.00	.46	19.1	—	60	—	2
<i>Rubus parviflorus</i>	16.8	—	1.00	.51	16.2	5.2	85	50	2
SAXIFRAGACEAE									
<i>Ribes viscosissimum</i>	13.1	7.8	1.00	.51	16.2	5.2	85	40	2
<i>Tiarella unifoliata</i>	13.1	—	1.00	.63	12.0	—	85	47	2
SCROPHULARIACEAE									
<i>Pedicularis racemosa</i>	12.5	7.5	1.00	.51	16.2	5.2	65	35	2
VALERIANACEAE									
<i>Valeriana sitchensis</i>	7.8	—	1.00	.98	5.2	—	45	30	2
VIOLACEAE									
<i>Viola glabella</i>	13.1	7.5	1.00	.63	12.8	5.2	95	35	2
<i>Viola sempervirens</i>	13.1	—	1.00	.57	16.2	5.2	85	45	2

¹ Potential transpiration (PT) is calculated for April through September based on a minimum stomatal resistance of 4 sec cm⁻¹. Transpiration is expressed in g cm⁻².
The ratio of simulated transpiration (T) to potential (PT) reflects the degree of stomatal control exhibited by a reference conifer.

Plant Moisture Stress (PMS) is expressed in atm and represents predawn measurements on reference conifers near the end of the summer dry season (Sept.).

A Temperature Growth Index (TGI) reflects the potential for Douglas-fir seedling growth as a function of air and soil temperature for the entire growing season.

The soil tolerance index indicates whether the species is exclusively restricted (class 3), tolerant (class 1), or excluded (class 2) from infertile ultrabasic soils.

Values of 30 in PT and PMS columns indicate species are known to occupy environments more extreme than possible for coniferous forest.

Table 3.—Predicted plant response indices for 25 forest ecosystems based on the inclusive limits of species present with known ecological distributions¹

Forest type ²	Stand	PT, maxi- mum	PT, mini- mum	T/PT, maxi- mum	T/PT, mini- mum	PMS, maxi- mum	PMS, mini- mum	TGI, maxi- mum	TGI, mini- mum	Soil toler- ance
Black oak	3	21.4	17.7	0.29	0.29	25.4	25.4	98	95	1
Black oak	21 ³	21.4	17.7	.29	.29	25.4	25.4	96	95	1
Ponderosa pine	8	21.4	17.7	.42	.40	20.3	20.3	96	90	1
Ponderosa pine	12 ³	16.8	13.5	.62	.46	19.1	12.6	70	68	1
Mixed conifer	1	13.5	13.5	.62	.51	15.3	5.2	75	68	2
Mixed conifer	11	16.8	13.5	1.00	.57	15.3	5.2	70	68	1
Mixed conifer	13	13.1	12.2	1.00	.63	12.8	8.4	80	68	1
Mixed conifer	19	13.1	12.2	1.00	.63	12.8	5.2	84	68	2
White fir	2	12.5	12.2	.62	.51	15.3	12.6	65	50	1
White fir	9	12.5	12.2	.63	.57	16.2	12.8	59	60	2
White fir	14 ³	13.1	11.0	1.00	.63	12.8	8.4	70	52	2
White fir	22 ³	13.1	10.3	.62	.63	12.8	5.2	70	52	2
Shasta red fir	7 ³	7.8	7.8	1.00	.98	5.2	5.2	45	45	2
Shasta red fir	16	12.5	7.5	1.00	.51	15.3	5.2	59	40	1
Shasta red fir	17	7.8	7.8	1.00	.98	5.2	5.2	45	45	2
Mountain hemlock	6	7.8	7.5	1.00	.98	5.2	5.2	45	35	2
Mountain hemlock	15 ³	11.0	7.5	1.00	.46	19.1	5.2	59	34	2
Mountain hemlock	18 ³	7.8	7.5	.62	.46	19.1	12.6	40	35	2
Mountain hemlock	24 ³	7.8	7.8	1.00	.98	5.2	5.2	45	44	2
Jeffrey pine	4	16.8	12.7	.61	.51	15.3	12.6	70	52	3
Jeffrey pine	5	19.5	12.7	.40	.40	18.1	12.6	70	52	3
Jeffrey pine	25 ³	19.5	12.7	.61	.51	15.3	8.4	70	52	3
Yew	20 ³	17.7	16.8	.51	.42	16.2	15.0	85	80	2
Engelmann spruce	23	11.0	11.0	.63	.63	12.8	12.8	47	47	2
Brewer spruce	10	10.3	7.8	.62	.46	19.1	12.8	50	50	2

¹ Potential transpiration (PT) is calculated for April through September based on a minimum stomatal resistance of 4 sec cm^{-1} . Transpiration is expressed in g cm^{-2} . The ratio of simulated transpiration (T) to potential (PT) reflects the degree of stomatal control exhibited by a reference conifer.

Plant Moisture Stress (PMS) is expressed in atm and represents predawn measurements on reference conifers near the end of the summer dry season (Sept.).

A Temperature Growth Index (TGI) reflects the potential for Douglas-fir seedling growth as a function of air and soil temperature for the entire growing season.

The soil tolerance index indicates whether the species is exclusively restricted (class 3), tolerant (class 1), or excluded (class 2) from infertile ultrabasic soils.

² From R. H. Waring, Forest plants of the eastern Siskiyou: their environmental and vegetational distribution, Northwest Sci. 43: 1-17, 1969.

³ Simulation of PT and T/PT was not possible because of inadequate data. The predicted values appear reasonable when compared with other stands with similar vegetation, temperature, and plant moisture stress indices.

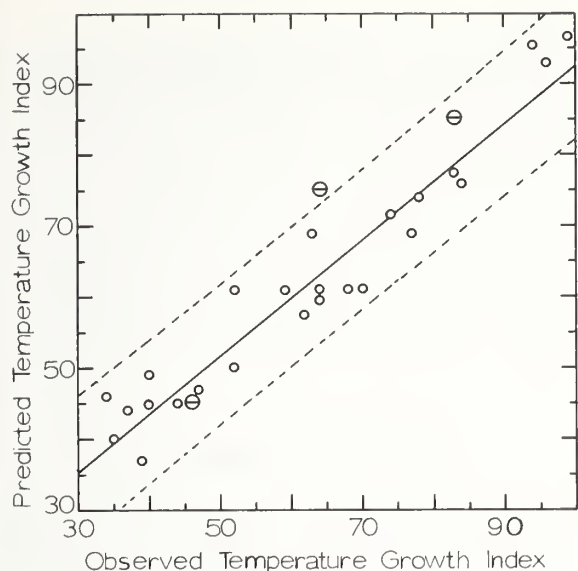


Figure 5. Relationship between the temperature index derived from the growth response of Douglas-fir to temperature and the midpoint values predicted from the presence of indicator species in a given ecosystem (table 3). Validation stands, Θ , with one exception fell within the 95-percent confidence limits. $r^2 = 0.93$.

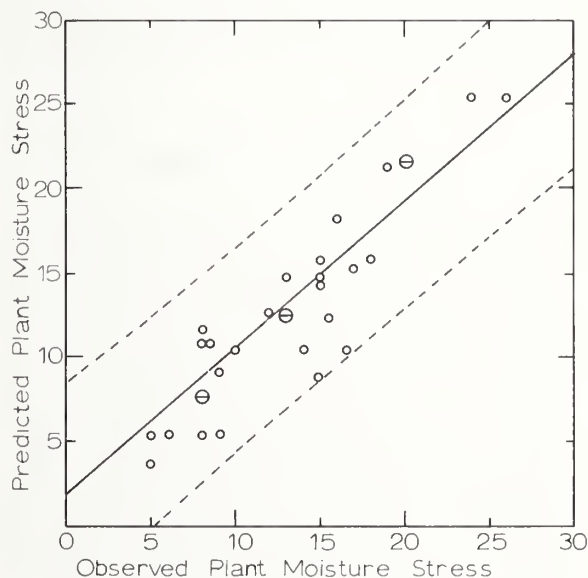


Figure 6. Relationship between the moisture stress index during the period when soil water may be limiting to reference conifers and the midpoint values predicted from the presence of indicator species in a given ecosystem (table 3). Validation stands, Θ , fell within the 95-percent confidence limits. $r^2 = 0.77$.

significant. Similarly, figure 6 presents the regression for plant moisture stress where the r^2 was 0.77, also highly significant. The symbol Θ represents validation stands which generally fell within the 95-percent confidence intervals.

From the comparisons made earlier, we showed that environmental plant indices can predict the forest composition, and conversely from the above relationships, we note that environmental indices may be predicted from knowledge of the distribution of specific plants.

Environmental Plant Indices as Predictors of Forest Productivity

In this study the only index to productivity was maximum tree height. Particularly on the infertile ultrabasic soils, this index overestimates productivity, for although individual trees reach considerable height, the density of trees remains low. Reed and Waring¹ reported that the ratio of actual to potential transpiration (T/PT) combined with the Temperature Growth Index (TGI) accounted for 96 percent of the variation observed in the maximum height of Douglas-fir. For all dominant trees, these and related indices accounted for 86 percent of the variation in height. The model for analytic solution is:

$$\begin{aligned} \text{Maximum height (in meters)} = & \\ & - 102.3 + 0.334 \text{ PT} + 316.4 \text{ T/PT} + 0.405 \text{ TGI} \\ & - 186.8 (\text{T/PT})^2 - 3.25 (\text{T/PT})\text{PT} + 0.631 (\text{T/PT})\text{TGI} \end{aligned}$$

This is encouraging, considering the limited sampling of tree heights and the expected differences among species. The model was not improved by including the index to soil fertility, again suggesting that total height may be an inadequate measure of productivity.

Data Requirements

If the environmental grid is to be applied across the Coniferous Forest Biome, then a coordinated effort must be made to test and improve the approach. Present efforts by

¹ Unpublished data.

Walker, Reed, Scott, and Webb are channeled toward providing additional physiological information on Douglas-fir, one of four proposed reference plants. These investigators are concerned with photosynthesis, water uptake, transpiration, and translocation. Lavender and Hermann are responsible for providing functional relationships between foliage, stem, and roots. Through stem and twig analysis and by aging foliage, we hope to gain measures of net primary production.

Other reference plants include *Pinus ponderosa*, *Tsuga heterophylla*, and *Abies lasiocarpa*; additional studies on these species are necessary.

To extend and validate the general approach described in this paper, we will require certain kinds of information at selected forest environments across the Biome. Forest stands will be selected which represent equilibrium stages; i.e., approach the maximum accumulation of biomass, on homogeneous areas at least 30 m².

Within these stands, bud break will be recorded on 1- to 2-m reference conifers by observing five lateral branches on each of at least five trees. Cambial activity will be assessed by using the pin-into-cambium technique which identifies the termination of cell divisions (Wolter 1968). Stand composition and structure will be estimated from basal area and height estimates of trees and understory sampling of shrub and herbaceous cover.

Nocturnal moisture stress will be measured on three to five reference trees at 2-week intervals throughout the growing season and at less frequent intervals during the dormant season, unless winter dessication is likely. Temperature under the stand near reference trees will be recorded at 1 m above and 20 cm below ground level. Latitude location of stands will allow for calculation of day length for different seasons. Nutrition will be assessed from a composite sample of 1-year-old foliage collected from the lateral branches of at least five trees at the time of new shoot elongation and during the late fall.

Short wave radiation will be measured in a nearby open area or above the stand. Data will be expressed in cal cm⁻² day⁻¹. Absolute humidity will be measured daily at solar noon

during the growing season and if possible continuously year around. Precipitation will include both monthly values and average maximum snow depth. Estimates of wind velocity are desired where conditions appear to warrant measurements.

These data will not only be valuable to help construct the environmental grid but will serve to interpret process studies in decomposition, consumer population dynamics, and other ecosystem properties.

Acknowledgments

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*Water and Nutrient
Movement Through Ecosystems*

Modeling water movement within the upper rooting zone of a Cedar River soil []

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Abstract

The Richards equation for unsaturated soil water flow is used to represent flow in a natural forest soil. The differential equation and the corresponding finite difference technique used to obtain an approximate solution are discussed. Independent estimates of soil moisture conductivity and of initial soil water content at several depths are used as inputs to the finite difference equation. Conductivity was estimated by laboratory techniques, and initial conditions in the field were measured by tensiometer. A tension lysimeter system provided estimates of soil water flow. Predicted values were compared with values measured in the field. Results suggest that the model gives a satisfactory representation of actual soil water flow despite considerable variability in forest soil properties.

Introduction

In the Coniferous Forest Biome, we have been interested in models which represent the movement of water through unsaturated soils for use as possible components of a larger computer model which describes water relations within a local soil-plant-atmosphere system. Other components of the larger model include uptake of water by the roots of trees, conduction of water through the vascular system to the leaves, and transpiration from the leaves to the surrounding atmosphere. When we find that existing submodels can be used—possibly with slight modifications—in our larger soil-plant-atmosphere model, we prefer to use them rather than to invent them anew. Where existing models are not well suited to our objectives, we prefer to develop new ones. For example, we are currently constructing a model which represents the flow of water through the vascular system of a tree. We evaluate existing or new sub-

models on the basis of (1) their behavior in isolation and (2) their compatibility with other components of the system. In the present paper we report our experiences with the Richards equation, a model which describes the flow of water in an unsaturated soil.

The Model

The Richards equation (Richards 1931) is essentially a modification of the well-known Darcy relationship for saturated flow in porous media. Because the Richards model allows for variation in hydraulic conductivity with changes in soil water content, it is well suited for the description of water flow in unsaturated media. Darcy's law with variable conductivity and negative hydraulic head can be written (Rose 1966)

$$v = K \frac{\partial \psi}{\partial \theta} \frac{\partial \theta}{\partial z} - K \quad (1)$$

Here v is the volume of water crossing a unit area per unit time (cm/min).

K is the hydraulic conductivity (cm/min),

ψ is the soil water pressure or suction (hydraulic head) (cm),

θ is the soil water content (volume of water per unit volume of soil), and

z is the height above datum (reference level) of the point under consideration (cm).

By introducing the concept of soil-water diffusivity, defined by

$$D = -K \frac{\partial \psi}{\partial \theta},$$

where D is measured in cm^2/min , Childs and Collis-George (1950) cast the Darcy equation in a form similar to Fick's law of diffusion:

$$v = -D \frac{\partial \theta}{\partial z} - K \quad (2)$$

Applying the equation of continuity, $\frac{\partial \theta}{\partial t} + \frac{\partial v}{\partial z} = 0$ (which implies that there are no sources or sinks of water in the system), one obtains the full Richards soil flow equation:

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left(D \frac{\partial \theta}{\partial z} \right) + \frac{\partial K}{\partial z} \quad (3)$$

Soil moisture is obtained as a function of depth (z) and time (t) by integrating (3). Accordingly the Richards model is compatible with our larger soil-plant-atmosphere model, which requires soil moisture at various depths and times as an input to a submodel which represents the uptake of water by the roots of a tree. Our current uptake model is that of Gardner (1960), a diffusion-type flow equation in which time rate of change of soil water concentration (θ) at any point (z) in the soil is related to the moisture gradient between that point and an absorbing root.

Since D and K depend on θ , (3) is nonlinear in θ , and a solution is possible only if numerical approximations are used. Remson et al. (1965) developed a computer program which gives approximate results when initial moisture content is specified at each of $n+1$ equally spaced points or nodes into which a soil column z_n centimeters thick is divided for

purposes of calculations. Soil moisture specified as a function of time is required at the upper and lower boundaries of the soil column. Their solution permits the simultaneous calculation of

$$\left(\frac{D_j + D_{j+1}}{2} \right) \left(\frac{\theta_{j+1} - \theta_j}{z_{j+1} - z_j} \right), \quad j = 1, 2, \dots, n$$

This expression approximates $D \frac{\partial \theta}{\partial z}$ and hence v , the volume flux of water, apart from the constant K (cf. equation 2).

Available Observational Data

At the Allan Thompson Research Center, Cedar River Watershed, the downward flow of water through soil profiles has been measured for several years by a tension lysimeter system (Gessel and Cole 1965). A prescribed suction on the porous lysimeter plate causes drainage through the plate to approximate the drainage in the adjacent soil. Results are recorded in permanent form on paper tape by an automatic data recording system. Our data come from a series of controlled experiments, carried out in 1970, which were designed to study the effects of rainfall on wetting fronts in the rooting zone of a Douglas-fir stand. Lysimeter plates were installed at depths of 11 and 25 cm and rainfall was simulated by a below-canopy sprinkler system. Soil moisture was measured by tensiometer at a point midway between the soil surface and the upper lysimeter plate, and water flux through the lysimeter was recorded by a flow meter connected to the data recorder.

For the present study only the data for the 11-cm plate were used. Since an abrupt change in the physical characteristics of the soil occurs between the 11- and 25-cm levels, a different set of estimates of the conductivity and diffusivity parameters is required for the lower layer. A model coupling the flow of water through the two layers has been developed but has not yet been tested.

Parameter Estimation

In order to estimate conductivity (K) and diffusivity (D), both of which are functions of soil water content (θ), we used standard laboratory and computational procedures (Richards 1948, Green and Corey 1971). The so-called moisture release curve, a plot of ψ against θ , was also obtained in the laboratory. Curves for K, D, and ψ as functions of θ are shown in figure 1.

Our Cedar River core samples of the Everett gravelly sandy loam were biased to an unknown degree by the removal of the large stone fraction before the laboratory analysis. These stones constitute perhaps up to 20 percent of the volume of the Everett soil series. Because these stones tend to impede the flow of water in unsaturated soils—the path around them is longer than it would be for smaller obstructions—we believe our estimates of K may be somewhat too large. This decrease in conductivity associated with the presence of large stones is especially noteworthy if the soil is highly unsaturated because water strongly held by matric forces flows only along capillary paths around the stones and not directly through the interstices of aggregations of large stones and cobbles.

Since conductivity of water in unsaturated soils is extremely difficult to measure directly, it has become common practice to estimate this parameter from pore-size distribution data, or equivalently, from the soil moisture release curve. Green and Corey (1971) have reviewed three methods for calculating K based on pore-size distribution and found that all give good results when compared with measured data. Our curve for K as a function of θ is based on laboratory measurements of K for the saturated Everett soil and adjusted for unsaturated soils by use of the Marshall pore-interaction relationship with a matching factor (Marshall 1958).

The shape of the moisture release curve is also affected by sampling procedures. Removal of large stones clearly biases the results in the direction of a soil with smaller pores. Accordingly, the correct relationship is somewhat to the left of the one determined in the

laboratory. This implies that the slope $\frac{\partial \psi}{\partial \theta}$ is different from that indicated by our laboratory data and that our estimate of the diffusivity $D = -K \frac{\partial \psi}{\partial \theta}$ is biased.

Computational Procedures

We used the Remson computer program, which provides an approximation to the solution of (3). As we have already noted, it is possible to calculate at the same time an approximation to the volume flux of water, $v = -D \frac{\partial \theta}{\partial z}$, at any depth in the soil. For this calculation initial moisture content must be specified at a number of equally spaced points, called nodes, along the vertical soil profile. Our nodes were set at depths of 1, 3, 5, 7, 9, and 11 cm. Initial moisture content was measured at approximately 5.5 cm by tensiometer. The lysimeter plate at 11 cm depth provided another point of known moisture content. Because suction at the lysimeter plate was maintained at a constant level, the moisture content at that point could be obtained directly from the empirically determined moisture release curve. Estimates of initial values at other nodes were obtained by linear extrapolation. Moisture content at the upper boundary (the soil surface) varied with incoming precipitation.

Results and Discussion

Observed flow of water through the lysimeter plate is compared to that predicted by the flow equation in figures 2, 3, and 4 which summarize the outcomes of three field experiments, and the corresponding computer runs. The results follow a consistent pattern. Predicted and observed flows begin, peak, and subside at about the same time. Maximum predicted flow is about 25 percent greater than observed. At lower levels of flow the correspondence is closer.

We conclude that the Richards flow equa-

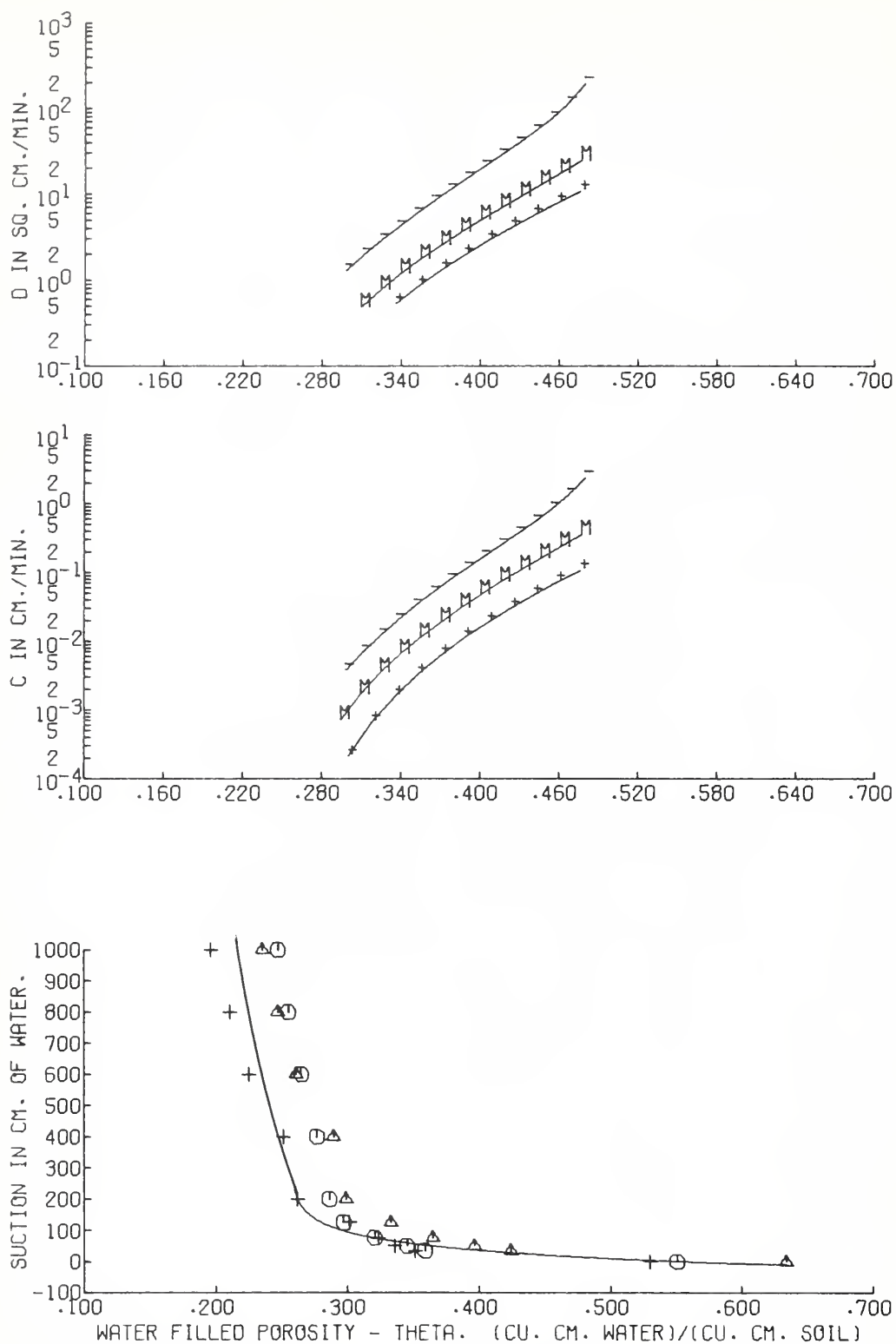


Figure 1. Soil water diffusivity (top), conductivity (middle), and suction (bottom) as functions of soil moisture content (θ). Everett gravelly sandy loam. M indicates mean values used in model. Three samples were used to obtain the moisture-release curve.

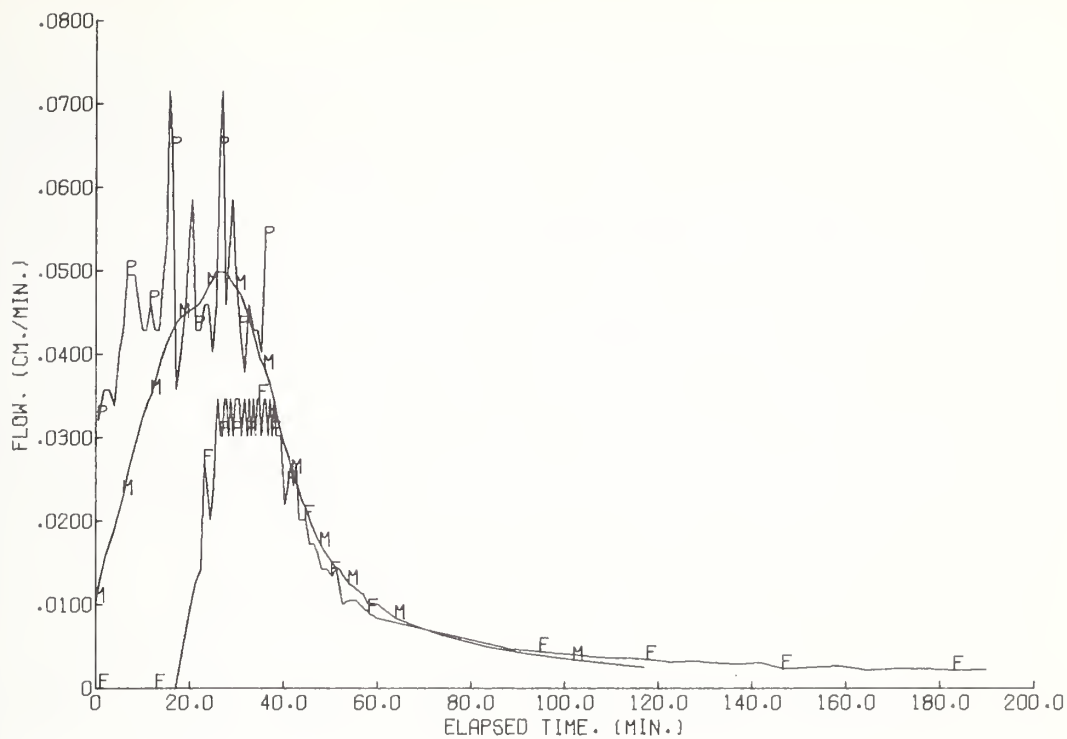


Figure 2. Precipitation (P), observed soil water flow (F), and modeled soil water flow (M) at 11 cm. Lysimeter suction was 50 cm of water.

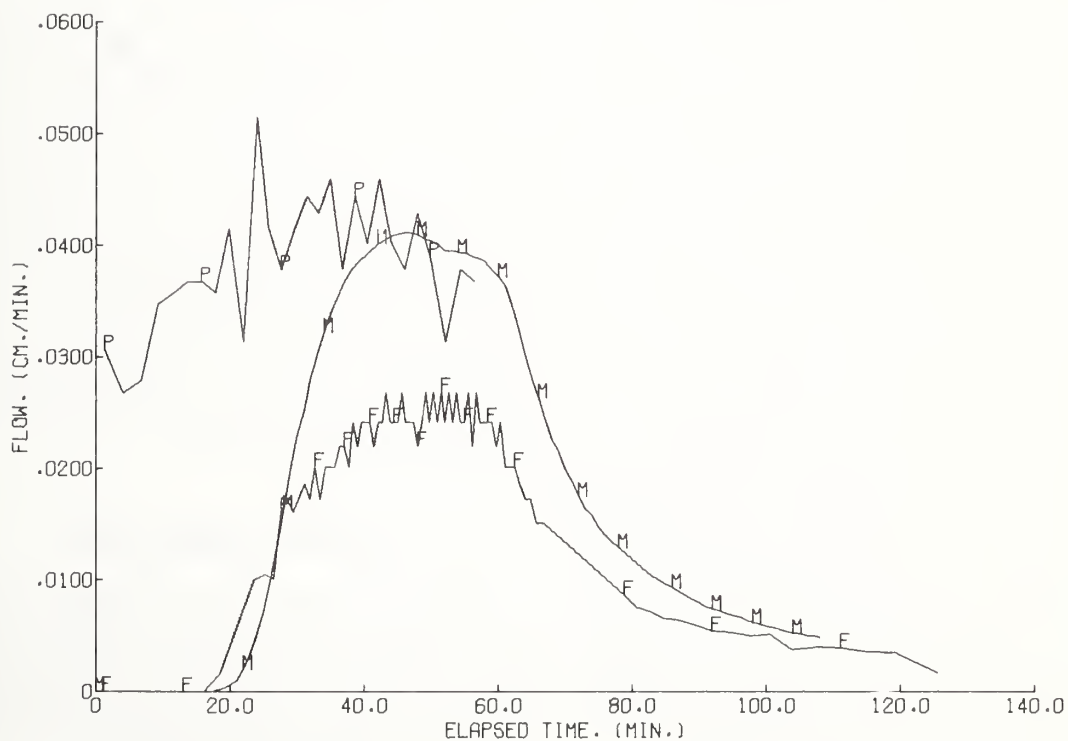


Figure 3. Precipitation (P), observed soil water flow (F), and modeled soil water flow (M) at 11 cm. Lysimeter suction was 88 cm of water.

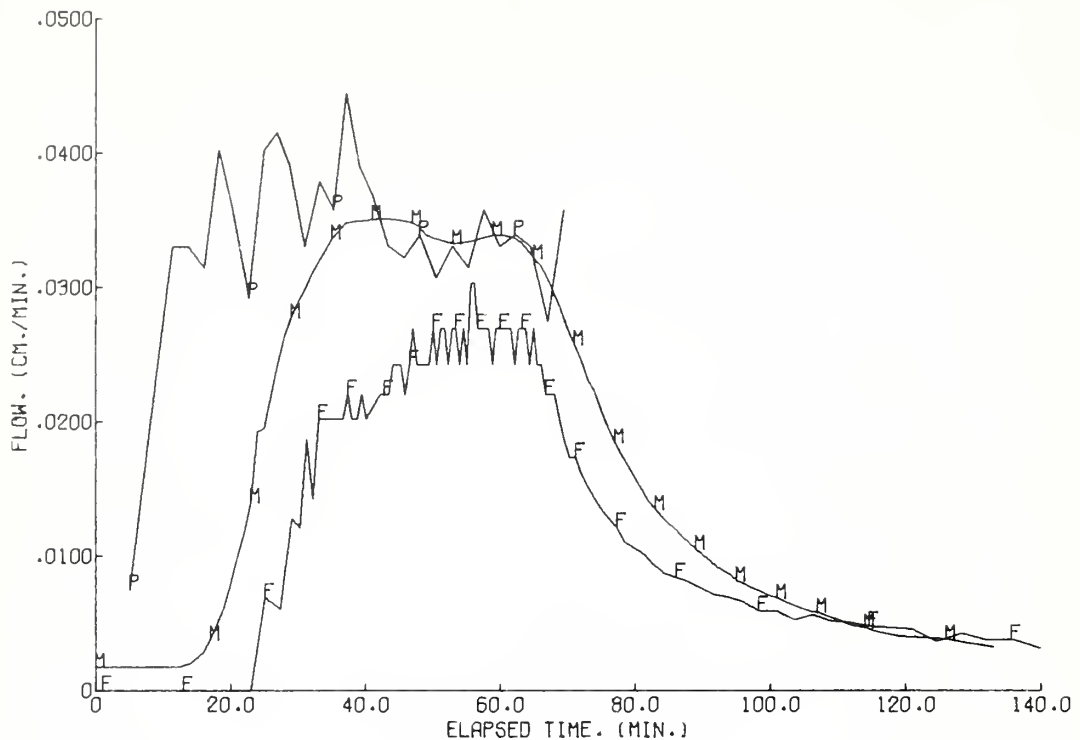


Figure 4. Precipitation (P), observed soil water flow (F), and modeled soil water flow (M) at 11 cm. Lysimeter suction was 146 cm of water.

tion provides a satisfactory description of the flow of water in the upper rooting zone of our Douglas-fir stand. Since the Everett gravelly sandy loam is extremely variable, our results probably should not be extrapolated much beyond the local area in which they were obtained.

We have not been able to account for the 25 percent discrepancy between predicted and observed peak flows. A number of possible explanations have occurred to us. It can be argued that the lysimeter system is not a perfect device for measuring water flow in a vertical column of soil. For example, in the early stages of a flow experiment, acceleration of flow due to lysimeter suction may be greater than that due to gravity. Perhaps more significant may be variations in flow associated with the lack of homogeneity of an in situ forest soil. We suspect that stones or roots in soil above the lysimeter plate diverted water toward or away from the plate. Perhaps more important, our estimates of initial values of θ at several nodes are not accurate.

It is probably more important to emphasize that the field experiments described here were conducted for purposes rather far removed from our present one of evaluating the Richards equation as a possible component of a soil-plant-atmosphere model. We also wish to point out that the Richards equation has not received adequate evaluation in field situations, perhaps because the stringent underlying assumptions are rarely satisfied. The rather close correspondence between model and observation that we have obtained suggests that the model may be more robust than has been generally believed.

Acknowledgments

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Elemental transport changes occurring during development of a second-growth Douglas-fir ecosystem

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Abstract

Mineral cycling processes in a second-growth Douglas-fir ecosystem have been monitored for nearly 10 years at the A. E. Thompson Research Center in western Washington. In this interval, substantial year-to-year differences in quantities of elements transferred have been observed. For example, a comparison of transfers during the 1964-65 and 1970-71 measurement years showed that input of calcium by precipitation increased roughly 300 percent while calcium transfer by throughfall, stemflow, and leaching from the forest floor increased roughly 600 percent, 350 percent and 220 percent, respectively. In the same interval, the mass and elemental content of the standing crop increased roughly 15 percent while forest floor mass and elemental content remained constant. A portion of this difference is related to the increased mass accumulated in the standing crop. However, the major factor causing this large difference is climatic variation. These differences in elemental transfer indicate the need for continuous observation of transfer processes to resolve the effects of ecosystem development on mineral cycling against this background of climatic variation.

Introduction

The growth and development of a coniferous forest ecosystem does not normally occur in a steady linear fashion. Rather, intervals of rapid stand growth may be interrupted by periods of slower growth reflecting changes in growing conditions. In turn, the cycling of elements within a forest ecosystem can be expected to reflect these changes.

Intensive study of the mineral cycling processes in second-growth Douglas-fir stands has been in progress at the A. E. Thompson Research Center since 1961. During this time, a substantial body of information has been collected concerning the amounts, pathways, rates of transfer, and mechanisms controlling

transfer of elements by the mineral cycling processes of this ecosystem. Between 1961 and 1966, research was concentrated largely on detailed descriptions of ecosystem components (Cole, Gessel, and Dice 1967).

Research at the Thompson site since 1966 has had two major objectives: (1) to provide information describing the changes in mineral cycling processes as the stand grows and (2) to examine the year-to-year variation in mineral cycling processes. More recently, a third objective has been to examine the relationships between climatic factors and the various mechanisms controlling rates of transfer along the different transfer pathways.

During the course of research at the Thompson site, a number of changes in the

patterns of elemental cycling have been observed. Some of these changes are related to changes in the structure or mass of the ecosystem; other changes are related to short-term variations in climatic factors. The purpose of this paper is to examine several of the changes in mineral cycling processes as they have been observed during the 10 years of research at the Thompson Research Center.

Experimental Area

These studies were conducted at the A. E. Thompson Research Center, an area specifically developed for the study of elemental cycling in second-growth Douglas-fir stands. It is located about 64 km southeast of Seattle, Washington, at an elevation of 215 m in the foothills of the Washington Cascades. A full description of the geology, soils, vegetation, and climate is given by Cole and Gessel (1968).

The study site is located on a glacial outwash terrace along the Cedar River. This outwash terrace was formed during the recession of the Puget lobe of the Fraser ice sheet about 12,000 years ago.

The soil underlying the research plots is classified as a typic haplorthod (U.S. Department of Agriculture 1960) and is mapped as Everett gravelly, sandy loam. This soil contains less than 5 percent silt plus clay and normally contains gravel amounting to 50-80 percent of the soil volume. The forest floor is classified as a duff-mull (Hoover and Lunt 1952) and ranges from 1 cm to 3 cm thick. This forest floor represents the accumulation since 1931 when the present stand was established following logging (around 1915) and repeated fires.

The present overstory vegetation is a planted stand of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) which was established about 1931. Currently, the trees average about 19 m high with a crown density of about 85 percent.

The principal understory species are salal (*Gaultheria shallon* Pursh), Oregon grape (*Berberis nervosa* (Pursh) Nutt.), red huckleberry (*Vaccinium parvifolium* Smith), and

twinflower (*Linnaea borealis* L. ssp. *americana* (Forbes) Rehder). Various mosses are the principal understory vegetation beneath the denser portions of the canopy.

The climate is typical of foothill conditions in the Puget Sound Basin. Temperatures have ranged from -18°C to 38°C , but these extremes are seldom reached. The average temperature for July is 16.7°C and for January is 2.8°C . The average annual precipitation is 136 cm, almost all falling as rain. Precipitation rates are generally less than 0.25 cm/hour and over 70 percent falls between October and March.

Field Plots

The facilities at the research site are designed to provide precision measurement of the flux of elements within this forest ecosystem. Some transfers are monitored continuously; others, with less potential for rapid change, are measured at regular intervals. A detailed description of the collection facilities at this site is given by Cole and Gessel (1968). The following section will briefly describe these facilities with emphasis on recent changes in the system.

Sampling

Precipitation collections are made at two locations in the stand. One collector is at the top of a 30-m tower and is fitted with a flowmeter; the other is an automatic collector (Wong Laboratories) which opens at the onset of precipitation and is mounted on a 10-m tower in a clearcut adjacent to the plots.

Canopy drip (foliar leaching) is collected in six randomly located screened funnels mounted in the necks of collection flasks. Stemflow is diverted from the stem of the six sampled trees at breast height (1.35 m) by soft rubber collars and is collected in covered 160-liter polyethylene trash cans. Litter is collected on eight randomly located 0.21 m^2 plastic litter screens. Leaching through the forest floor and soil is measured using the tension lysimeter system developed by Cole (1968). This system permits direct measure-

ment of the flux of ions through the soil. In this plot, 3 lysimeters per soil horizon are located in the soil at the base of the forest floor, at the base of the A₁ horizon (4 cm) and B₂ horizon (30 cm) and at 100 cm in the C horizon.

Instrumentation

Meteorological measurements including air and soil temperature profiles, are made on a continuous basis utilizing a data logging system. Details of this instrumentation are given by Cole and Gessel (1968).

The data logging system also permits the continuous monitoring of the pH and conductivity of water moving through this ecosystem. These facilities are described by Cole (1968). Volumes of water flow between different components of the system are measured using the resistance flowmeter described by Cole (1968).

Chemical Analysis

Analytical methods used on samples from this site have changed over the years. For methods used in earlier studies, the reader may consult the following reports: Rahman (1964); Cole and Gessel (1965); and Cole, Gessel, and Dice (1967). The methods currently in use will be briefly described in the following paragraphs.

Water Analysis

Determinations of calcium, magnesium, potassium, and sodium are normally made directly on water samples using an Instrumentation Laboratories-353 atomic-absorption spectrophotometer. Calcium is determined in a nitrous oxide-acetylene flame; and magnesium, potassium, and sodium are determined in an air-acetylene flame. Nitrogen and phosphorus are determined from a hydrogen peroxide-sulfuric acid digest (Linder and Harley 1942) of a 10-fold concentration of the solutions. Nitrogen is determined using a micro-Kjeldahl distillation (Jackson 1958). Phosphorus is determined using the chloro-

stannous-reduced molybdophosphoric blue color method of Jackson (1958). Total ion concentration is estimated from specific conductance using an empirical method (Logan 1961) and pH is determined instrumentally using established methods. Further details of water analysis are given by Grier (1972).

Soil Analysis

Total soil nitrogen is determined using the standard Kjeldahl digest and distillation of Jackson (1958). Cation exchange capacity is determined using the neutral ammonium acetate leaching method (Jackson 1958). Exchangeable cations are determined spectrophotometrically from the ammonium acetate leachate. Soil carbon is determined instrumentally using a Leco carbon analyzer. Phosphorus is extracted from the soil by digestion in 36 N sulfuric acid and 30 percent hydrogen peroxide; concentrations are then determined following the same procedures as for water samples.

Tissue and Forest Floor Analysis

Elemental assays of forest floor and plant tissue are done using methods described by Grier and McColl (1971).

Results and Discussion

Table 1 shows how organic matter, calcium, potassium, nitrogen, and phosphorus were distributed among different components of the ecosystem at the Thompson site at the end of 1965 (Cole, Gessel and Dice 1967). Since the time of this determination, transfers between these various components have been monitored to assess the changes and rates of change of elemental distribution in the stand.

In the interval between 1966 and the present, the volume of woody tissue in the stand has increased by an average of 11 m³/ha/yr⁻¹. This represents approximately a 15-percent increase in volume since 1966. Increases in mass and elemental content of most components of the standing crop are estimated—using estimation procedures developed for

these stands by Dice (1970)—to be proportional to the increase in woody tissue mass. However, the foliar mass has probably remained about constant in this interval. Thus at the present time, the quantities of elements and organic matter in the standing crop at this site are about 15 percent greater than shown in table 1.

In the same interval, other components of

the ecosystem have shown relatively little change. For example, the forest floor was intensively sampled in 1961,¹ 1965 (Cole, Gessel, and Dice 1967), and 1969 (Grier and McColl 1971). Results of these studies are summarized in table 2. With the exception of magnesium content, the forest floor of this

¹D. W. Cole. Unpublished data on file at the College of Forest Resources, University of Washington, Seattle.

Table 1.—Distribution of N, P, K, Ca, and organic matter (g/m²) in a 35-year-old second-growth Douglas-fir ecosystem at the Thompson Research Center (Cole, Gessel, and Dice 1967)

Component		N	P	K	Ca	Organic matter
TREE						
Foliage	current	2.4	0.5	1.6	0.7	199.0
	older	7.8	2.4	4.6	6.6	710.7
Branches	current	.4	.1	.3	.2	51.3
	older	4.0	.9	3.2	6.5	1,337.3
	dead	1.7	.2	.3	3.9	814.5
Wood	current	1.0	.2	1.0	.4	748.5
	older	6.7	.7	4.2	4.3	11,420.2
Bark		4.8	1.0	4.4	7.0	1,872.8
Roots		3.2	.6	2.4	3.7	3,298.6
Total tree		32.0	6.6	22.0	33.3	20,452.9
SUBORDINATE VEGETATION						
		.6	.1	.7	.9	101.0
FOREST FLOOR						
Branches		.5	.1	.4	.8	142.3
Needles		3.5	.4	.5	2.7	300.5
Wood		1.4	.2	.8	1.7	634.5
Humus		12.1	1.9	1.5	8.5	1,199.9
Total forest floor		17.5	2.6	3.2	13.7	2,277.2
SOIL						
0-15 cm		80.9	116.7	7.9	31.3	3,837.2
15-30 cm		86.8	119.5	6.6	19.6	3,693.5
30-45 cm		76.1	98.0	5.2	15.2	2,829.0
45-60 cm		37.1	53.6	3.7	8.0	795.5
Total soil		280.9	387.8	23.4	74.1	11,155.2
TOTAL ECOSYSTEM		331.0	397.1	49.3	122.0	33,986.3

Table 2.—Forest floor composition changes during an 8-year period in a Douglas-fir ecosystem at the Thompson Research Center

Year sampled	g/m ²					
	Dry weight	N	P	Ca	Mg	K
1961	1,542	15.4	2.2	11.2	3.8	2.4
1964	1,500	16.1	2.4	12.0	3.7	2.4
1969	1,430	14.0	—	12.3	1.9	2.7

ecosystem has changed only slightly since 1961 indicating that litterfall is balanced by decomposition. Similarly, there has been no significant change in elemental capital in the soil (table 3) due both to the large reserves of most nutrients in this soil and to efficient cycling processes within the ecosystem. The decrease in magnesium capital in the forest floor between 1965 and 1969 may indicate increased rates of internal redistribution of magnesium within the standing crop. However, this is doubtful in view of the small change in magnesium capital in the soil (table 3).

The quantities of cations transferred between components of the ecosystem generally increased between 1964-65 and 1970-71 (table 4). Comparison of some transfers during the 1970-71 measurement year with those of the 1964-65 measurement year (table 4) reveals some rather substantial differences in both the overall amounts transferred and in the relative importance of the various pathways.

For example, input of calcium and potassium by precipitation is roughly four-fold greater now than in 1964-65. This increase may reflect a general increase in atmospheric pollution in the Puget Sound basin. The quantities of calcium and potassium returned to the soil from the aboveground vegetation have also increased since the 1964-65 measurement. As an example, return of calcium and potassium by stemflow has increased 25- and 35-fold, respectively, since measurement during 1964-65. Increases in return by foliar

leaching also were observed (table 4) but these were not of the same magnitude as the increased return by stemflow. No explanation has been found for the differential increases in return by stemflow and foliar leaching.

Return of elements by litterfall also increased between 1964-65 and 1970-71 (table 4). These differences are probably due both to normal year-to-year fluctuation of litterfall and also to the increasing proportion of branch material observed as a component of the litter.

Increases were also observed in leaching of elements through the soil profile. Leaching of calcium and potassium from the forest floor roughly doubled between 1964-65 and 1970-71 (table 4). A portion of this increase may result from increased rates of litter decomposition as well as the increased input in precipitation.

As previously noted, the forest floor mass appears to have approached a steady state condition (table 2); the present mass representing a quasi-equilibrium state, achieved since the stand was established in 1931, after repeated fires through the area. On the other hand, litterfall quantity has increased during the period of observation of this stand. In table 5, monthly litterfall measured at this site in 1962-63 (Rahman 1964) is compared with measurements made during 1970-71; the annual mass of litterfall has apparently increased roughly 50 percent over this 8-year period. Thus the increased quantities of ele-

Table 3.—Elemental capital in the soil of a second-growth Douglas-fir ecosystem at the Thompson Research Center as determined in 1965 and 1971

Depth	g/m ²				
	N	P	K	Ca	Mg
A) 1965:					
0-15	81	117	7.9	31	3.7
15-30	87	120	6.6	20	3.5
30-45	76	98	5.2	15	2.5
45-60	37	54	3.7	8	1.2
Total soil	281	389	23.4	74	10.9
B) 1971:					
0-15	86	123	8.3	40	3.2
15-30	82	111	6.6	21	3.3
30-45	71	104	5.3	10	2.7
45-60	40	52	4.2	11	1.5
Total soil	279	390	24.4	82	10.7

Table 4.—Transfers of elements between components of a Douglas-fir ecosystem at the Thompson Research Center during two stages of development¹

Item	Calcium (g/m ²)		Magnesium (g/m ²)		Potassium (g/m ²)		Sodium (g/m ²)	
	1	2	1	2	1	2	1	2
Precipitation	0.28	0.93	ND	0.22	0.08	0.47	ND	1.68
Throughfall	.35	2.05	ND	.49	1.07	2.83	ND	2.59
Stemflow	.11	3.85	ND	.60	.16	4.00	ND	2.30
Litterfall	1.11	1.78	ND	.20	.27	.47	ND	.07
Leaching from forest floor	1.74	3.87	ND	1.10	1.05	2.60	ND	2.18

¹ 1=transfers measured during 1964-65 measurement year. Reported by Cole, Gessel and Dice (1967).
2=transfers measured during 1970-71 measurement year.

Table 5.—Monthly amounts of litterfall during two intervals in the development of a second-growth Douglas-fir ecosystem

Month	Quantity (g/m ²)	
	1962-63	1970-71
October	73.0	89.0
November	17.9	44.5
December	9.2	14.2
January	6.5	10.0
February	15.9	3.8
March	6.2	13.8
April	7.4	5.8
May	12.8	(¹)
June	11.4	(¹)
July	5.2	39.1 ¹
August	5.5	21.0
September	12.3	41.6

¹ Litterfall amounts for May, June, and July 1971 are combined in July collection.

ments leached from the forest floor are at least partially due to increased litter decomposition rates.

Many of the changes in amount and relative importance of the transfer pathways since 1965, are probably due to changes in the mass and structure of this forest ecosystem. However, many of the changes are completely out of proportion to estimates of increased mass of the standing crop.

Observations made since 1966 at the Thompson site indicate that the return of elements to the soil and their subsequent distribution through the soil profile is sensitive to certain climatic factors; primarily precipitation and temperature. Variations in these climatic factors have been observed to cause substantial variation in quantities transferred along most pathways. As an example, the return of elements to the soil by stemflow and foliar leaching were found to be partially regulated by the distribution of precipitation; especially precipitation occurring during the summer. Figure 1 shows the monthly return

of potassium by stemflow from one tree for 1970 and 1971; the total amounts transferred being 0.50 gm during 1970, and 0.75 gm during 1971. Much of the greater amount returned during 1971 was returned during a few summer rainstorms. Foliar leaching, although not shown, exhibits a similar pattern of behavior. Apparently the extent of removal of potassium and other elements by leaching from Douglas-fir foliage is related to its phenological stage. This suggests that precipitation occurring in certain critical parts of the year may remove elements that would otherwise remain in the plant.

Temperature, the other major factor causing variation in year-to-year transfer rates, exerts its control on transfers primarily through its effect on organisms active in decomposition. Decomposer activity regulates the availability of nutrient elements in two ways; first, by regulating the rate of mineralization of elements and second, by its influence on levels of the mobile bicarbonate anion in the soil solution.

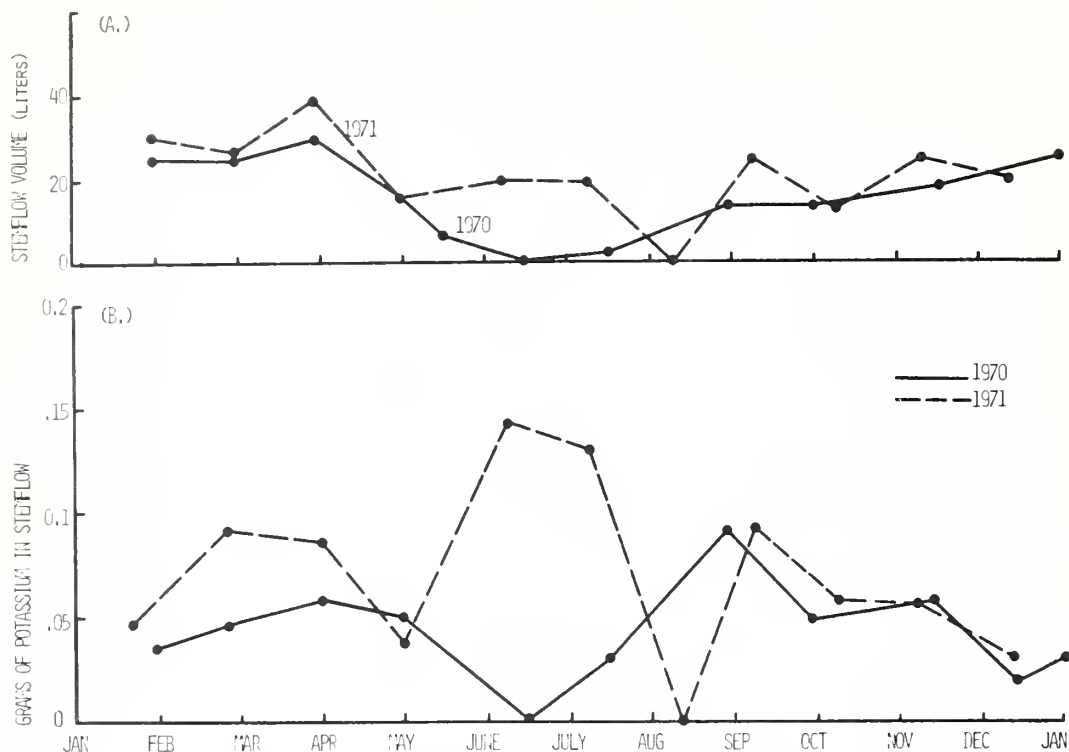


Figure 1.

A. Volume of stemflow from a 15-cm diameter Douglas-fir during 2 successive years.

B. Quantity of potassium transferred to soil from a single 15-cm diameter Douglas-fir during 2 successive years.

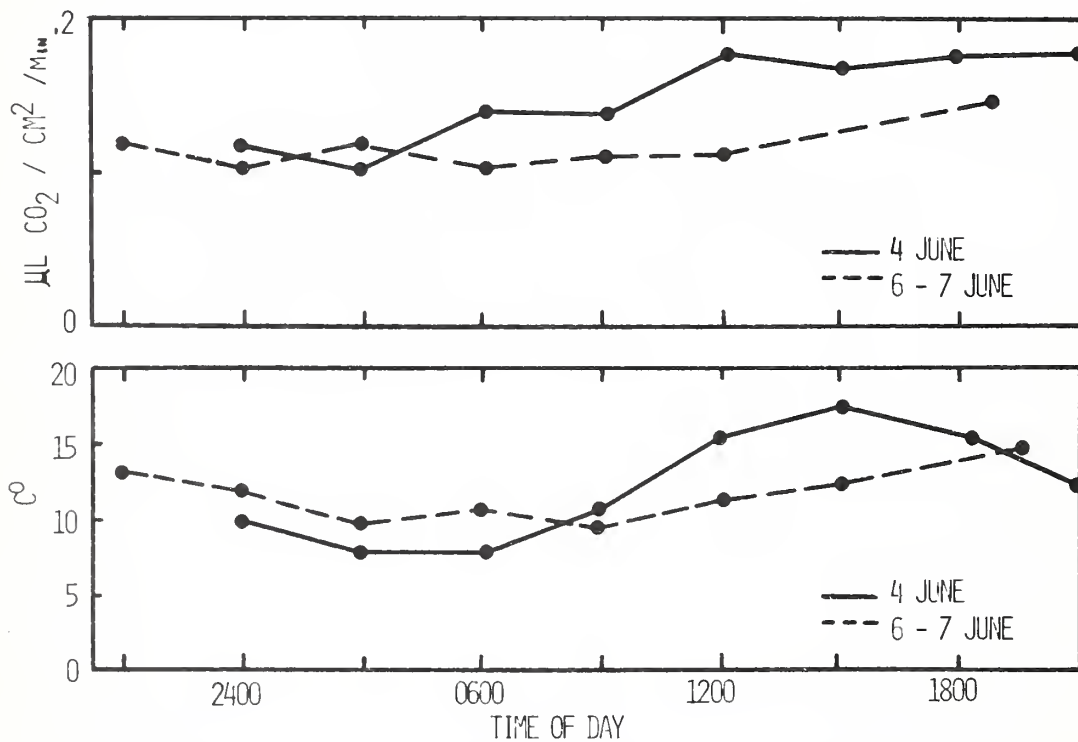


Figure 2. Temperature effects on CO₂ evolution from forest floor at Thompson Research Center (Ballard 1968).

Figure 2 illustrates how CO_2 production from the forest floor is related to temperature in this ecosystem (Ballard 1968). Temperature effects on mineralization rates are probably directly proportional to the temperature effects on CO_2 production rates.

The bicarbonate ion is the major anion in soil solutions at the Thompson site. Moreover, the concentration of this ion in the soil solution has been shown to be the major factor controlling rates of cation leaching in these soils (McColl 1969). Temperature effects on the levels of the bicarbonate ion are related to decomposer activity, since the equilibrium between CO_2 in the soil atmosphere and HCO_3^-

in the soil solution is related to CO_2 concentration. Consequently, leaching rates in the soil of the Thompson site are strongly related to temperature (McColl 1969).

Figure 3A illustrates the relationship between estimated ion concentration in forest floor leachates and air temperature. As can be seen from these data, the ion concentration closely follows temperature during the year. Monthly variations in mean ion concentration of forest floor leachates for 3 successive years (figure 3B) are primarily the result of differences in mean monthly temperature.

Total transfer by leaching is regulated both by temperature and the amount and date of

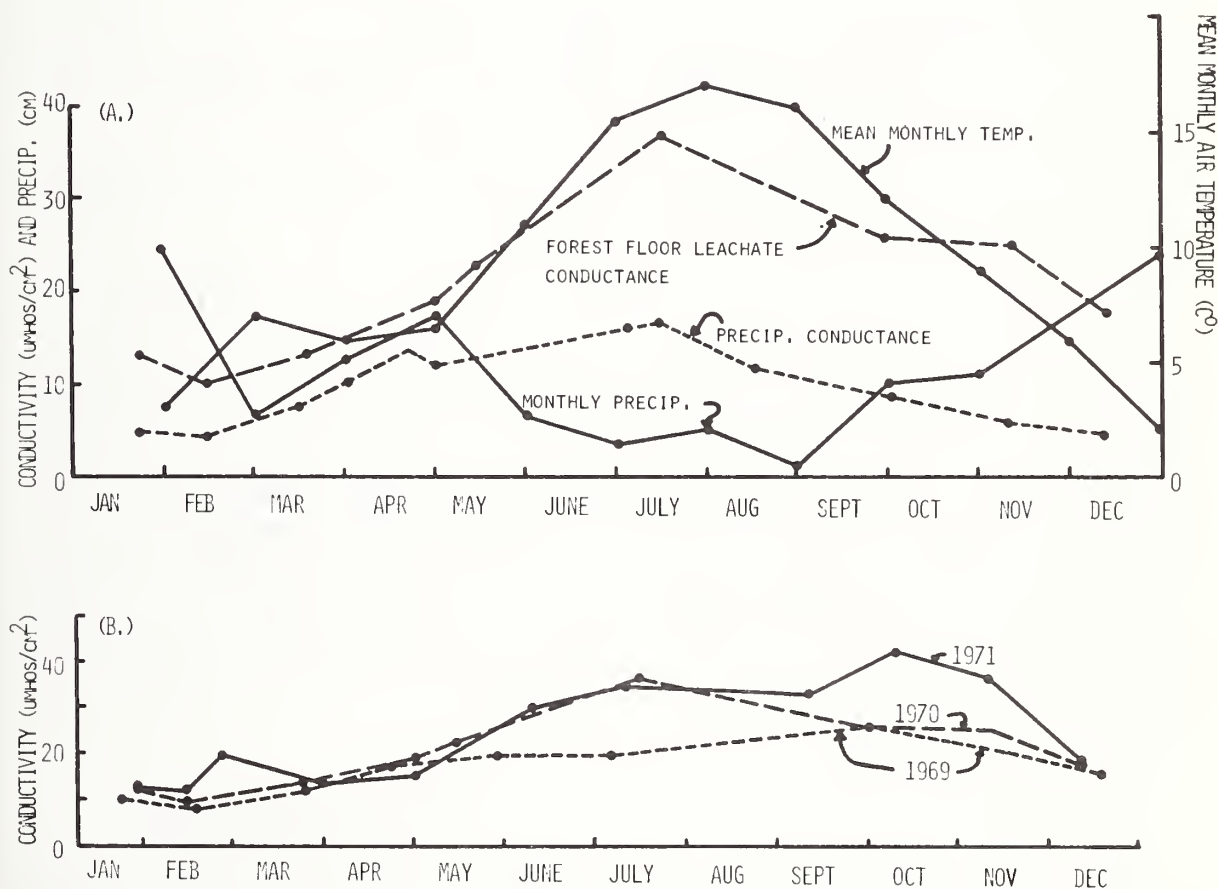


Figure 3.

A. Mean monthly precipitation, air temperature, and specific conductance of precipitation and forest floor leachates for the Thompson site during 1970.

B. Specific conductance of forest floor leachates for 3 consecutive years at the Thompson site.

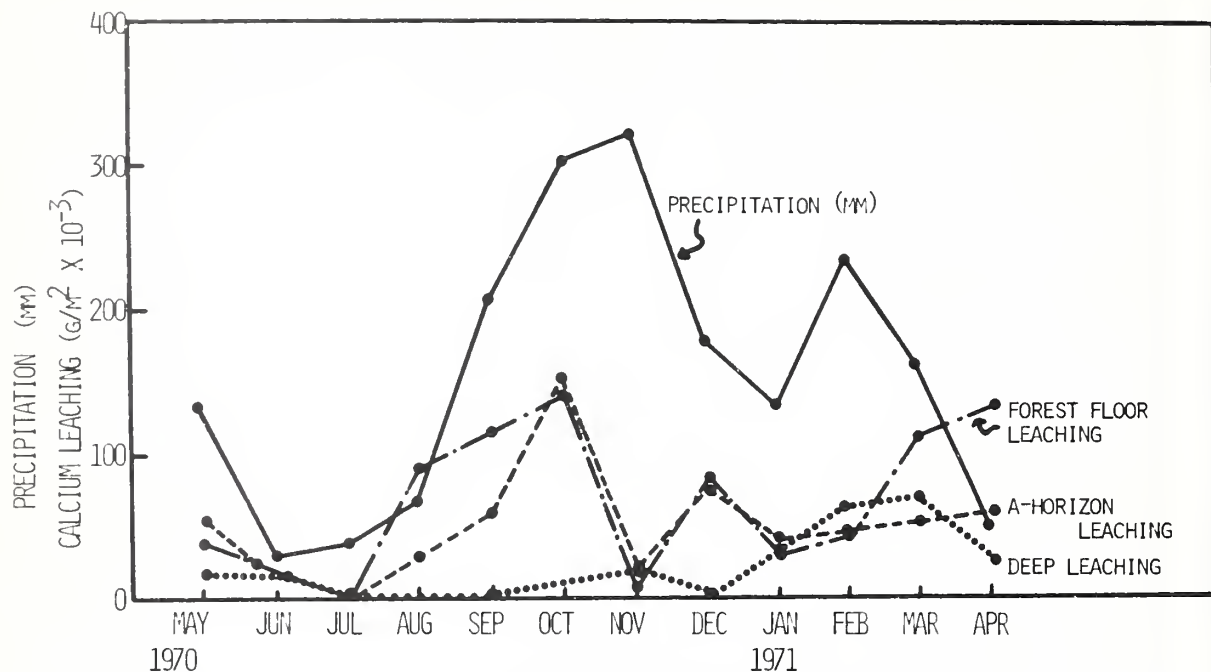


Figure 4. Rates of calcium leaching through soil profile and rate of precipitation during 1970-71 growing season.

occurrence of precipitation. The largest quantities of elements are transferred during periods of relatively high temperatures and ample precipitation. Figure 4 illustrates the relationship between leaching of calcium from the forest floor and A horizon of the mineral soil in 1970-71 and precipitation in that interval. As can be seen from these data, the greatest quantities of calcium were transferred during the spring and autumn when decomposer activity was relatively high and sufficient precipitation fell to flush the decomposition products into the soil.

Conclusions

Mineral cycling processes within a forest ecosystem are responsive to changes in the mass and structure of the standing crop and also to the shorter term effects of climatic variation. Of the two, the effects of climatic variation are the most readily seen. For this

reason, any efforts to describe mineral cycling processes within a forest ecosystem must include sufficient data that effects of changes in mass and structure of the ecosystem can be resolved and separated from the large year-to-year effects of climatic variability.

Present and future mineral cycling research at the Thompson site is directed towards separating and describing the possibly interdependent effects of growth and climate on mineral cycling processes in second-growth Douglas-fir.

Acknowledgments

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Nutrient budget of a Douglas-fir forest on an experimental watershed in western Oregon

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Abstract

Annual loss of nitrogen, phosphorus, silica, and the cations sodium, potassium, calcium, and magnesium followed the same pattern as annual runoff which is heavily dominated by winter rainstorms arising from the Pacific Ocean. Even though 170 and 135 cm of water passed through this Douglas-fir ecosystem for the 2 years reported here, this ecosystem conserved nitrogen effectively as indicated by an average annual dissolved nitrogen outflow of 0.5 kg/ha from an annual average input of 1.0 kg/ha in precipitation. There was a small annual net loss of phosphorus (0.25 kg/ha). Cation input in precipitation was less than 10 percent of sources from mineral weathering—indicating that mineral weathering was the principal source of cations to the system. Average annual net losses of calcium, sodium, magnesium, and potassium were: 47, 28, 11, and 1.5 kg/ha, respectively. Silica loss of 99 kg/ha-yr was the largest of all constituents and came entirely from within the forest system. Although loss of sediment was low during the period of study, loss of nutrients by soil erosion may become of major importance over a longer time scale due to widely spaced unsampled catastrophic erosion.

Introduction

The purpose of this study was to measure the inputs, losses, and retentions of specific plant nutrients.

Forested watersheds have been used for decades to study the hydrologic cycle. Bormann and Likens (1967) indicated that small watersheds are suitable for studies of chemical cycles if the ecosystem is located on a watershed with relatively impermeable bedrock. Then, all annual chemical fluxes into and out of the forest system can be attributed to a definable forest ecosystem, and errors due to deep seepage can be minimized. Small watersheds containing soil-plant systems have been generally accepted as useful units for ecological research.

Nutrient cycles begin with the establishment of vegetation, and the quantity of nutrients cycled undoubtedly increases as the

forest passes through successional phases. At all points, along this developmental sequence, the supply of nutrients in the soil-plant system is regulated by the balance between (1) the inputs from the atmosphere and mineral weathering and (2) the outflow by soil erosion or chemicals dissolved in stream water. A continued level of fertility of the system therefore depends upon the retention of nutrients in the cycle from loss by leaching and soil erosion.

Nutrient budget studies were begun on two small watersheds at the H. J. Andrews Experimental Forest in 1967. Only the initial results from one of these and the chemicals in solution will be reported here. The following questions were asked:

1. What quantities of nitrogen, phosphorus, the cations (sodium, potassium, calcium, magnesium), and silica reach the site in precipitation?

2. How effectively are these chemicals retained by the forest?
3. What hypotheses can be made about the processes that regulate the gain or loss of these chemicals from the forest?

The 10.1-hectare study watershed, designated number 10 in Forest Service studies, occupies strongly dissected topography characteristic of the west side of the Cascade Range. It rises from 430 m elevation at the stream gaging station to 670 m at the highest point on the back ridge. The overall slope is 44 percent, but side slopes and the headwall range up to 90 percent due to deep incision of the basin into the main ridge. Soils, from weathered tuff and breccia materials, have weakly developed profiles that often overlie saprolite up to 6 m deep. Tree roots are most abundant in the surface 0.6 m and probably do not penetrate much deeper than 2.4 m. The saprolite is porous and therefore can transmit water. The average annual precipitation is 230 cm.

Forest vegetation on the watershed consists of remnants of a 450-year-old Douglas-fir (*Pseudotsuga menziesii*) stand and islands of various younger age classes which originated when the old-growth stand was broken up by windthrow, disease, or fire. Because the basin is oriented toward the southwest, the side slopes within it face south, west, and north. A considerable diversity in vegetation on these slopes has recently been classified for the Experimental Forest by Dyrness, Franklin, and Moir (personal communication). Douglas-fir climax forests occupy ridgetop and upper slope south aspect positions on the watershed. A dense evergreen shrub layer, composed mainly of golden chinkapin (*Castanopsis chrysophylla*), Pacific rhododendron (*Rhododendron macrophyllum*), and salal (*Gaultheria shallon*) codominates the site beneath a sparse stand of old-growth trees. Western hemlock climax forests make up the remainder of the vegetation on the watershed. On these habitats, the dominant overstory is mainly Douglas-fir and western hemlock (*Tsuga heterophylla*). Proceeding from west to north aspects along a gradient of increasing moisture, the shrub cover shifts from vine maple (*Acer circinatum*)-salal, to rhododendron-

Oregon grape (*Mahonia nervosa*) and finally to vine maple-western sword fern (*Polystichum munitum*) on moist, north-facing middle and lower slopes.

Methods

Precipitation and streamflow are sampled by the following techniques. Precipitation at the top and bottom of the watershed is measured by standard rain gages; samples for chemical analysis are obtained from a special collector mounted on a tower 18 m tall in the center of a nearby clearcut. At the outlet of the watershed, an H-flume gages streamflow and a proportional water sampler, capable of sampling both dissolved and suspended materials from the stream, composites discrete water samples in a polyethylene carboy (Fredriksen 1969). The samples are removed at approximately 3-week intervals throughout the year. In 1970 and 1971, grab samples were taken from low summer flows; and during the winter of 1971-72, a series of grab samples were collected from streamflow during storm runoff events. In the laboratory, solids are removed by filtration through a fine glass fiber filter (Whatman GF/C) from both precipitation and streamflow samples and chemical analyses were performed on both fractions. The fraction that passes the filter is considered to be dissolved although we recognize that the filtered water may contain some particles smaller than 2 microns in diameter. Since the concentration of each chemical constituent is an estimate of the mean for the time during which the sample was collected, the input or loss for each sampling period is the product of precipitation or streamflow, respectively, and the concentration of each constituent.

Chemical analyses were done in duplicate as follows: Ammonium and dissolved organic nitrogen by distillation and digestion, respectively, on 1/2-liter samples and detection by Nesslerization; nitrite by the sulphanilamide method; nitrate by reduction and detection as nitrite; orthophosphorus by the molybdate blue method; total phosphorus by the molybdate blue method following a per-

sulfate-sulfuric acid digestion in the autoclave; reactive silica by the molybdate yellow method; cations sodium and potassium by flame emission; and calcium and magnesium by atomic absorption following addition of lanthanum as a masking agent.

Detection limits (mg/l) for the following chemicals were: organic nitrogen, 0.005; nitrate and nitrite, 0.0005; phosphorus, 0.005; sodium, 0.05; potassium, 0.1; calcium, 0.4; magnesium, 0.05; and silica, 0.1.

Results

Nutrient Input in Precipitation

Total amounts of nutrients dissolved in precipitation and the annual rainfall are given in table 1. Nitrogen enters the forest system mainly in organic substances; nitrate averaged only 13 percent of all nitrogen forms for the 2-year period. In that period, only trace amounts of ammonia nitrogen were detected, and a small quantity of nitrite in 1970. The

phosphorus came mainly in organic form in two collections in the fall of 1969. Of the cations, input of calcium was the greatest followed by sodium, magnesium, and potassium in descending order. Traces of silica were found in only five of the 14 collections in 1970.

There was also an input of particulate matter from the atmosphere that measured upwards of 3 to 5 kg/ha-yr. Although the average dustfall for 3 years was nearly equally divided between the dry season (April-October) and the wet season (November-March), the proportion in the wet season varied from 33 to 65 percent of the total for individual years.

Nutrient Loss in Streamflow

Nitrogen is transported in the stream almost entirely in the form of organic matter (table 2). Though water samples from this watershed were contaminated with nitrate from the exhausts of propane heaters, the nitrate nitrogen outflow from another un-

Table 1.—Nutrient input in precipitation for the period October 1 through September 30

Constituent in rainwater	1969	1970
----- kg/ha-yr -----		
NO ₃ -N	0.06	0.20
NO ₂ -N	0	.01
Organic N	1.02	.69
All N	1.08	.90
Ortho P	(¹)	.01
Total P	(¹)	.27
Na	1.17	2.34
K	.27	.11
Ca	7.65	2.33
Mg	.72	1.32
Si	(¹)	(²)
Precipitation (cm)	251	215

¹ Missing data.

² Trace.

Table 2.—Nutrient budget for dissolved constituents of precipitation and runoff for the period October 1 through September 30

Element	1969			1970		
	Input	Outflow	Net	Input	Outflow	Net
-----kg/ha-yr-----						
N	1.08	0.58	+0.50	0.90	0.38	+0.52
Total P	(¹)	(¹)	(¹)	.27	.52	-.25
Na	1.17	33.66	-32.49	2.34	25.72	-23.38
K	.27	1.24	-.97	.11	2.25	-2.14
Ca	7.65	53.65	-46.00	2.33	50.32	-47.99
Mg	.72	12.70	-11.98	1.32	12.44	-11.12
Si	(¹)	(¹)	(¹)	(²)	99.3	-99.3
H ₂ O-cm	251	170	81	215	135	80

¹ Missing data.

² Trace.

disturbed watershed nearby was 0.004 kg/ha-yr. A similar nitrogen outflow can be expected for the study watershed. Ammonium and nitrite do not occur in measurable concentrations.

Total phosphorus outflow, both organic and inorganic, was about in the same order of magnitude as outflow for nitrogen. The organic form predominates in spring, summer, and fall seasons but reaches minimum values in midwinter when the forest and soils are repeatedly flushed by rainwater. Orthophosphorus concentration remained nearly constant throughout the year, varying from 0.01 to 0.02 mg/l.

Cation and silica outflows were much larger than those of nitrogen and phosphorus. Potassium export was much smaller than that of other cations. Silica outflow was the largest of all the dissolved constituents. Transport of suspended sediment was 67 and 37 kg/ha-yr for 1969 and 1970, respectively.

Net Loss from the Watershed

The nutrient budget in table 2 results from the subtraction of the nutrient outflow in the stream and the input in precipitation. Net loss or gain is indicated by positive and negative values, respectively.

The small annual nitrogen gain of about 0.5 kg/ha was nearly the same for the 2 years. For all other mineral constituents of runoff, more was lost than was gained in precipitation. Phosphorus losses are relatively small and in the same order of magnitude as nitrogen losses. The cation and silica losses were from one to two orders of magnitude larger than those of nitrogen and phosphorus. Of the cations, calcium losses were greatest followed in descending order by sodium, magnesium, and potassium. Of all constituents, silica losses were greatest. Though precipitation and runoff were greater in 1969, the use of water by the forest was nearly equal for the 2 years.

Time Trends of Outflow and Concentration of Selected Chemicals

Movement of water in the forest system is obviously the dominant factor regulating the flow of chemicals. However, moderation of the annual chemical outflow pattern can be expected from processes such as organic decomposition, uptake into plants, and mineral weathering. These processes may be regulated by the hydrologic and thermal state of the forest system.

The time trends of soil temperature and water content are indicated on figure 1. Because precipitation occurs mainly during the fall and winter months with less than 2 percent of the annual total in July and August, substantial withdrawals of water from the soil are made by the forest during the summer. Water content of the top 30 cm of soil reaches minima, near the wilting point, usually in late August or early September. Fall rainstorms normally recharge the soil mantle to field capacity by the end of December, although recharge of the surface soil may occur from 1 to 2 months earlier. The soil temperature cycle is the inverse of the soil water cycle. Maxima near 14° C occur in August and minima from 0° to 2° C are common from December through March.

Precipitation and runoff for 1970 are illustrated in figure 2 for the periods that composite streamflow and precipitation samples were taken. Precipitation exceeded runoff by a wide margin in the fall of 1969 until soils reached field capacity sometime in late December or early January. The soil remained near field capacity until precipitation fell to low levels in early May. Wetting fronts from precipitation and snowmelt can pass through the soil mantle of the watershed during this period. Runoff declined rapidly with the increase of evapotranspiration and reduction of precipitation in the spring and summer months.

Organic nitrogen, calcium, and silica were chosen to illustrate the differences that exist in annual concentration and outflow patterns (figs. 3, 4, and 5). The influence of water can be seen immediately from the general correspondence of the stream runoff and chemical

outflow cycles. Minimum chemical outflow occurs in summer and fall while streamflow is low; maximum chemical outflow comes with high runoff in the winter months. However, the concentration patterns vary considerably between the three, and there are notable differences in outflow between organic nitrogen and the other two (calcium and silica) during the winter season.

Organic Nitrogen

The high concentration of organic nitrogen in October 1969 (fig. 3) came at a time when soils were dry (fig. 1) and could store all precipitation except that which falls directly into the stream or runs off rock and shallow soil areas adjacent to the stream. After a decline in early November (fig. 3), the concentration and outflow rose to a peak in December when soils probably had reached field capacity (figs. 1 and 2) and wetting fronts from precipitation could pass through the soil mantle. Organic nitrogen outflow remained high and reached a secondary peak in late January at peak runoff (fig. 3). As precipitation and runoff declined in February, concentration and outflow reached low values (figs. 2 and 3). The concentration and outflow rose again in late winter and early spring as precipitation increased (figs. 2 and 3). Outflow and concentration declined in April and May as precipitation declined and soil water storage dropped below field capacity (figs. 1, 2, and 3). Increased concentration in summer had little effect on outflow due to very low runoff (fig. 3).

Though the forest system retains more organic nitrogen than it loses (table 2), the gain is not uniform throughout the year. From mid-December to mid-February, the forest system lost more in outflow than it gained in precipitation; for the remaining 10 months, there was a net retention of organic nitrogen (fig. 6). For the 2-month midwinter period, the outflow in runoff (0.28 kg/ha) exceeded the input in precipitation (0.16 kg/ha) by 0.12 kg/ha. There was an increasing margin during the 2 months.

Contributions to the stream from the forest

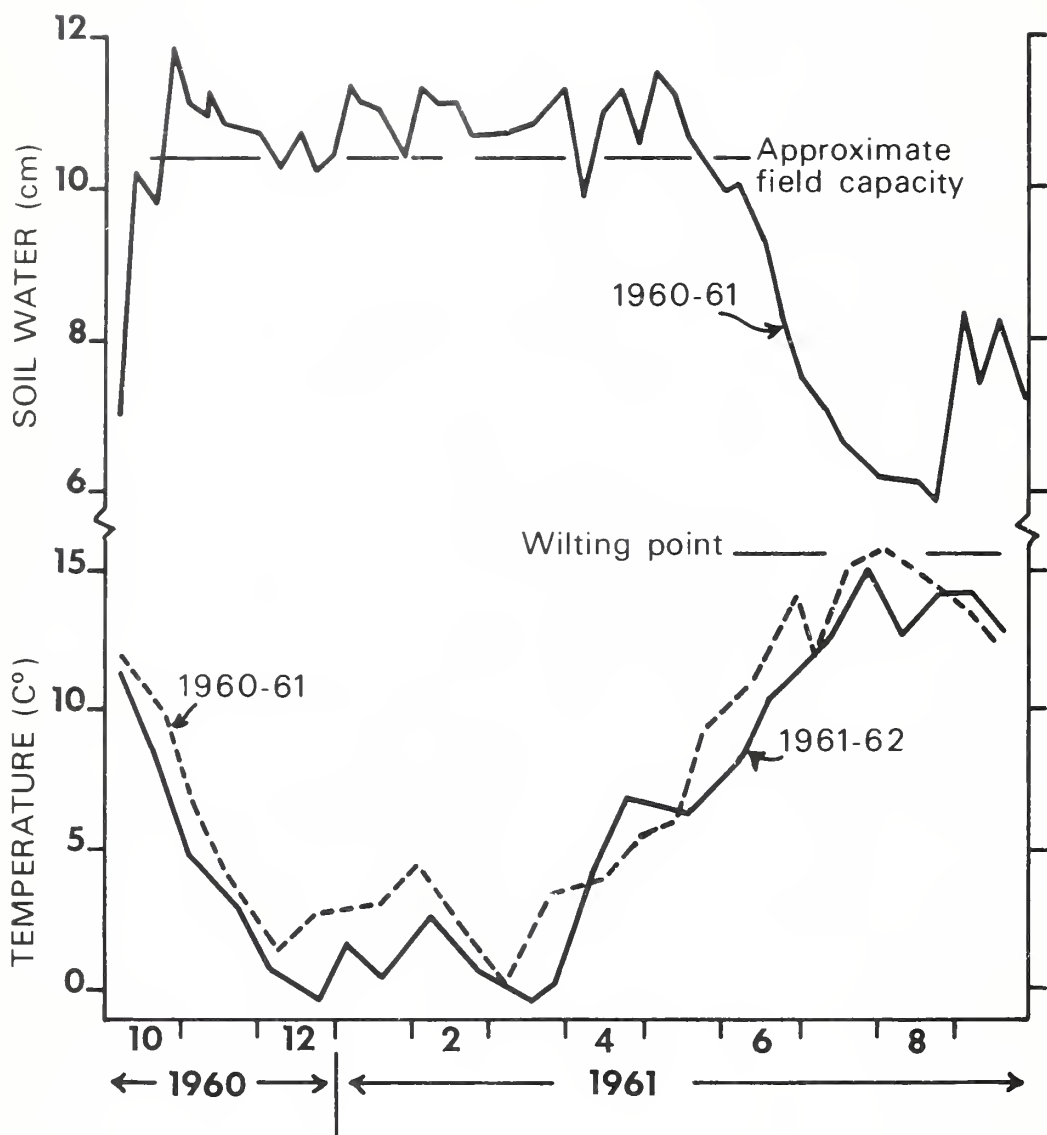


Figure 1. Water content of the surface 30 cm and temperature at 15 cm in the soil of an old-growth Douglas-fir forest.

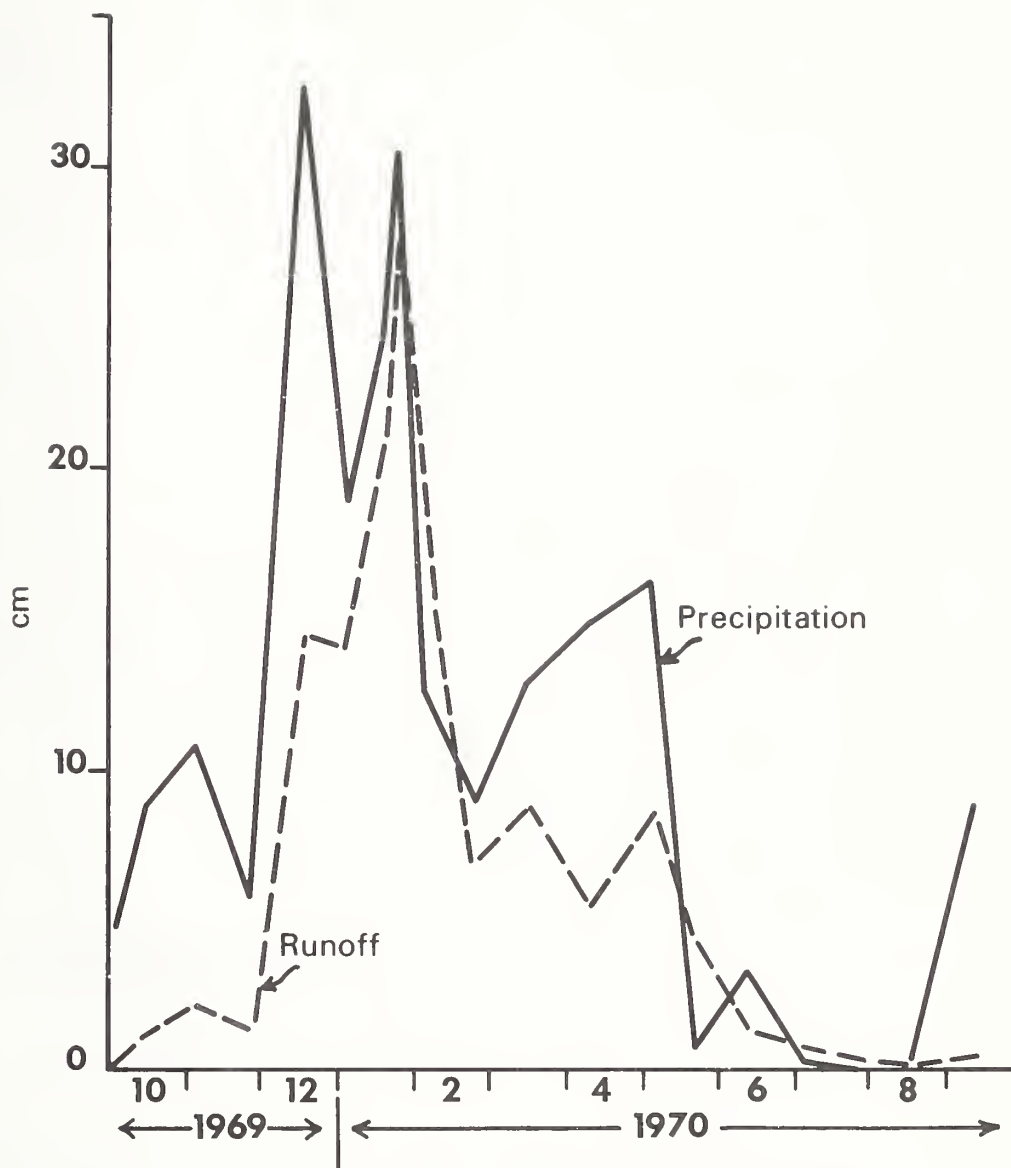


Figure 2. Precipitation and runoff for an undisturbed Douglas-fir forest for each sampling period, 1969-70.

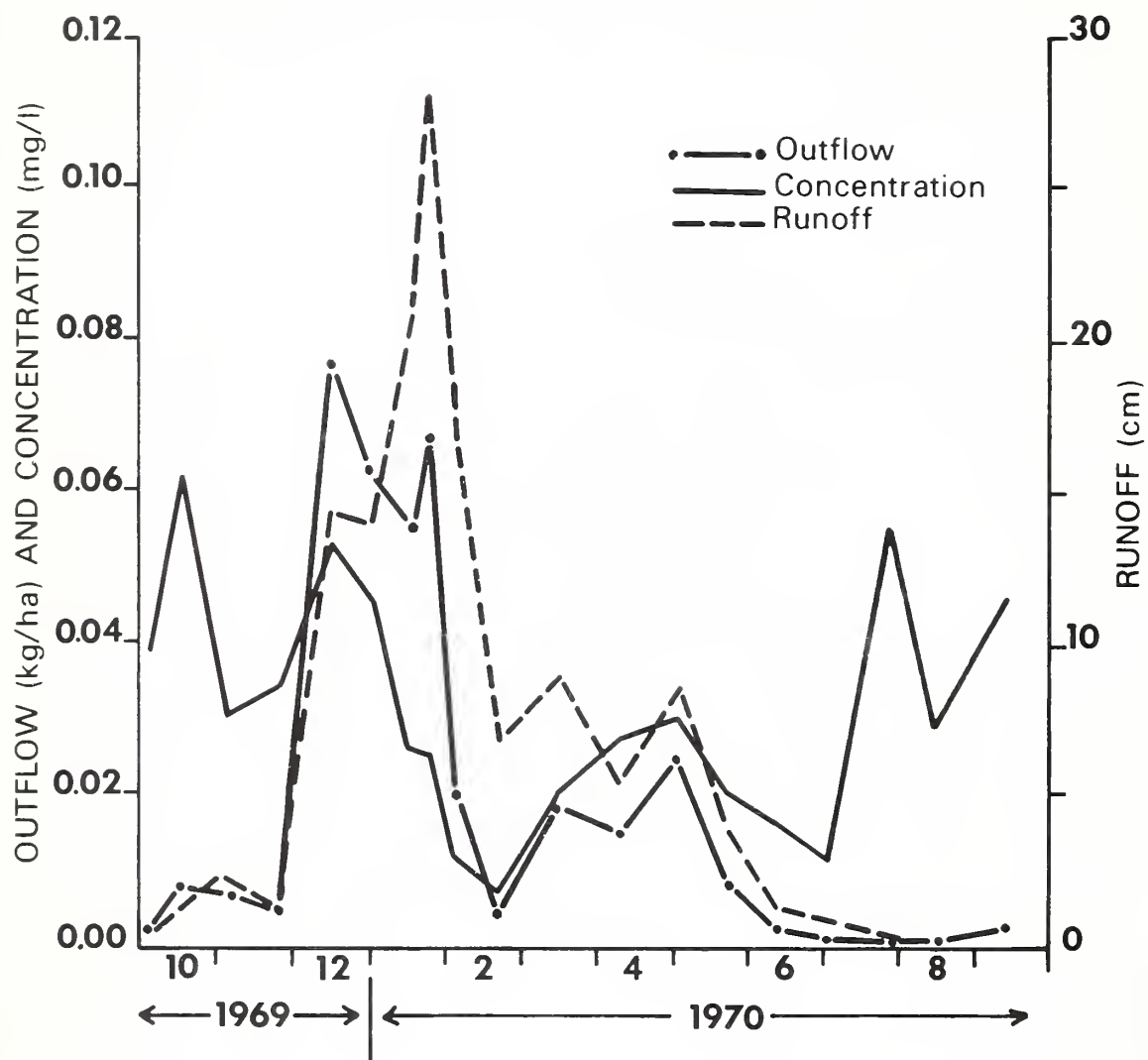


Figure 3. Concentration and outflow of organic nitrogen dissolved in stream water and runoff per sampling period from an undisturbed Douglas-fir forest, 1969-70.

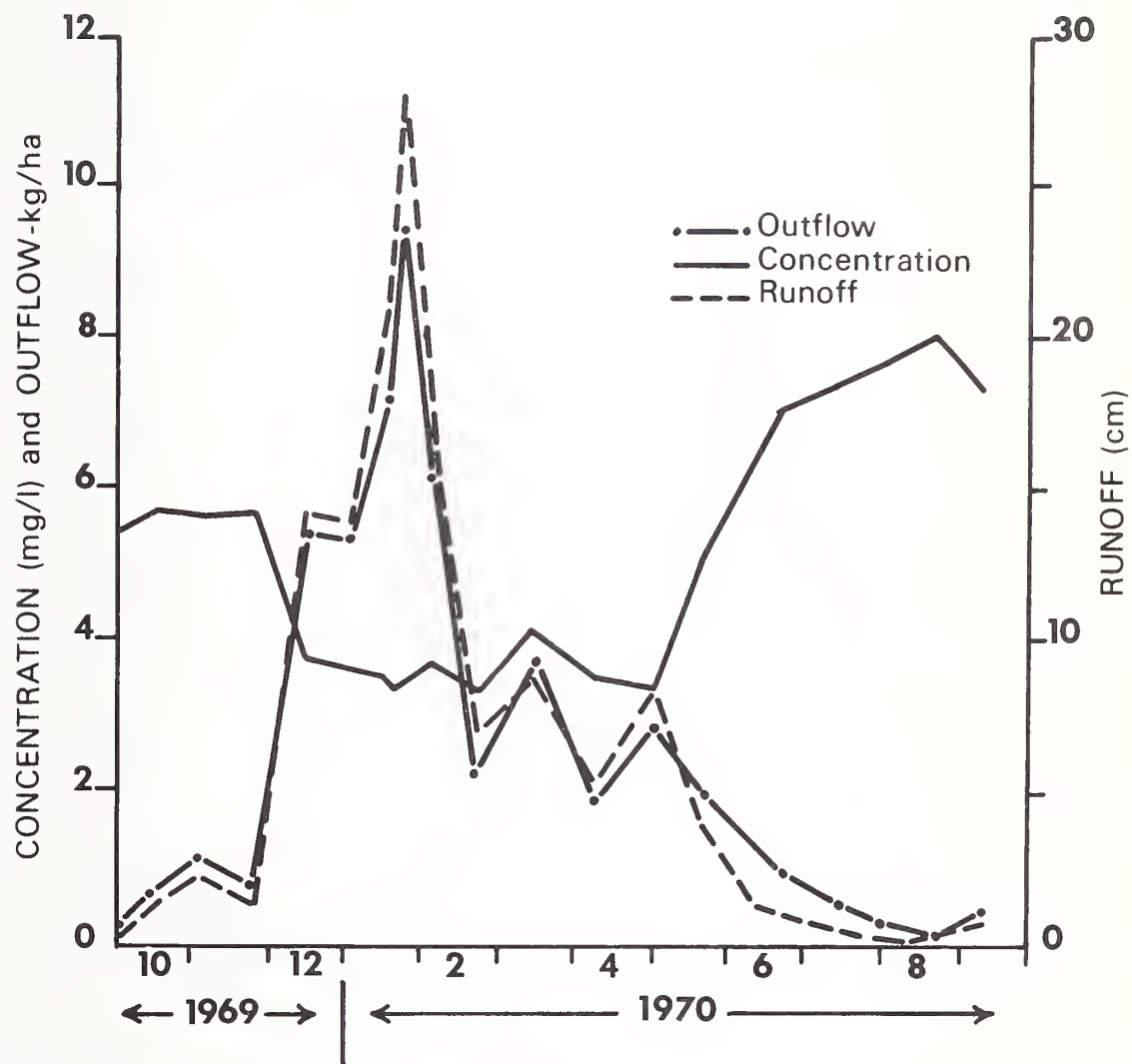


Figure 4. Concentration and outflow of calcium dissolved in stream water and runoff per sampling period from an undisturbed Douglas-fir forest, 1969-70.

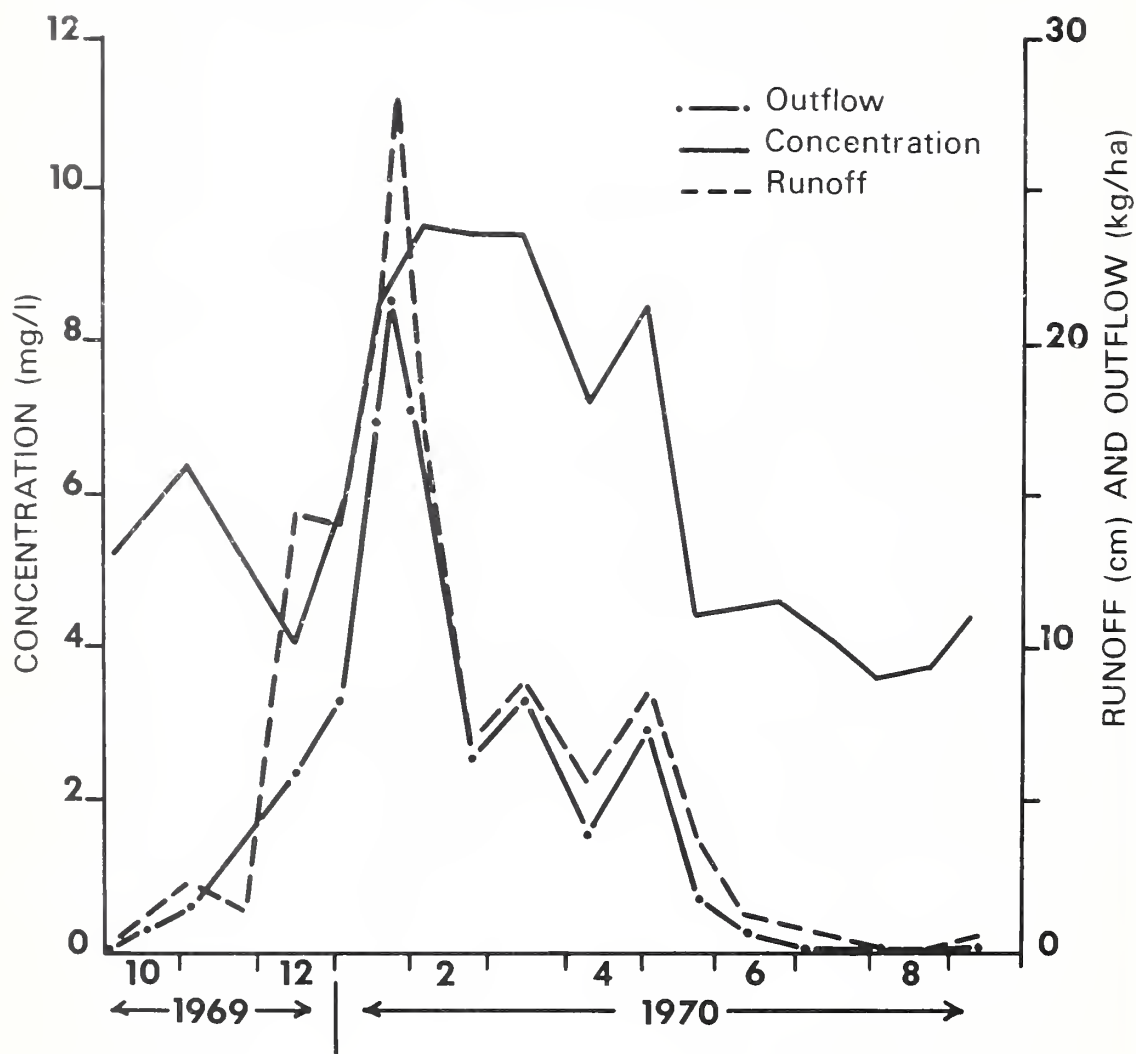


Figure 5. Concentration and loss of silica dissolved in stream water and runoff per sampling period from an undisturbed Douglas-fir forest, 1969-70.

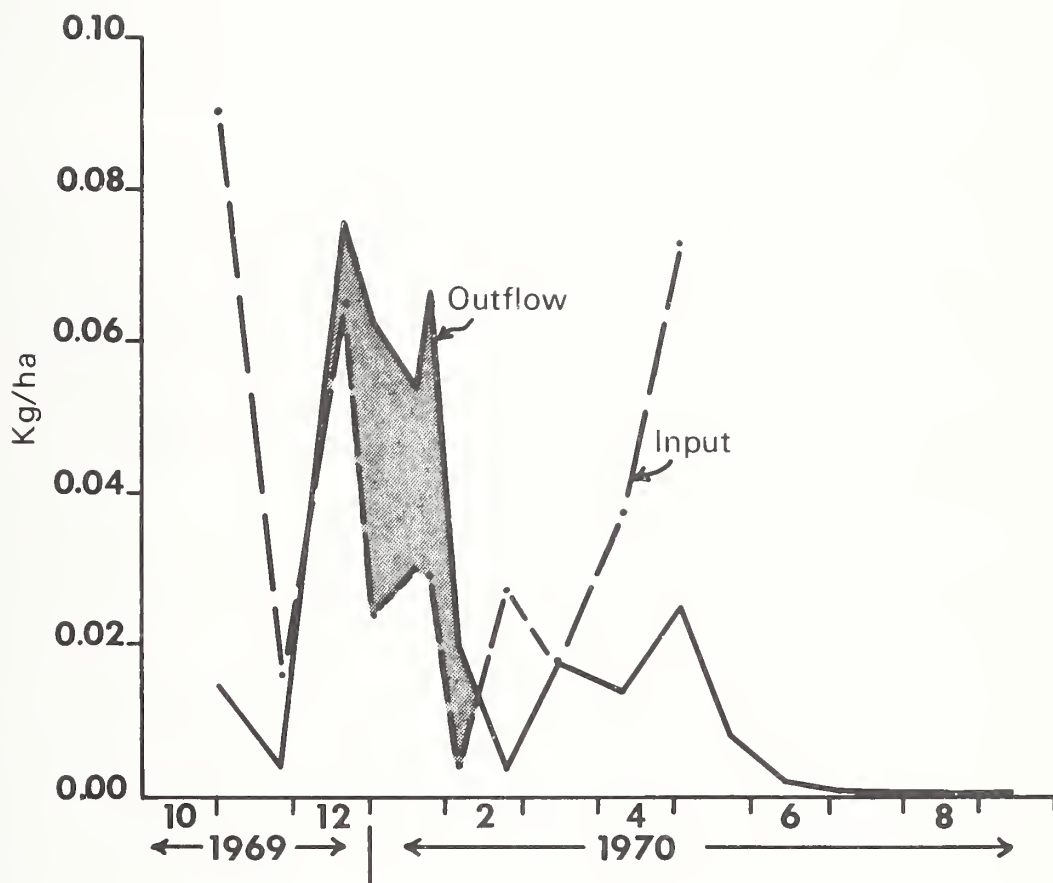


Figure 6. Input in precipitation and loss in runoff of dissolved organic nitrogen for each sampling period, 1969-70.

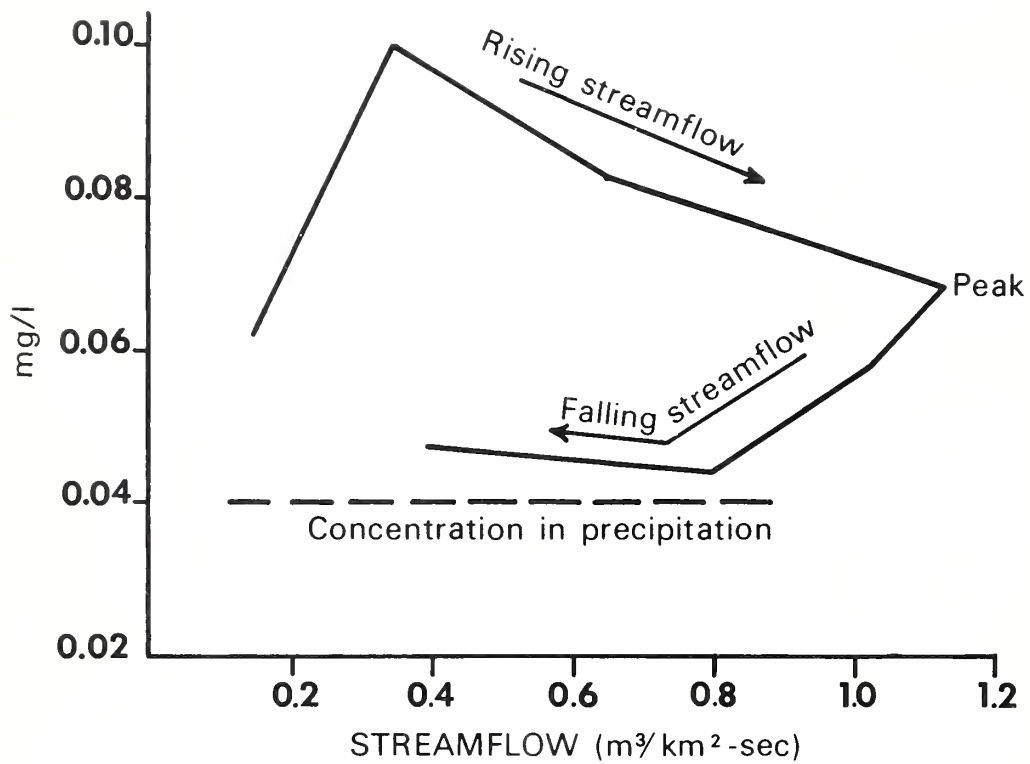


Figure 7. Concentration of organic nitrogen dissolved in streamflow during a storm runoff event November 25-29, 1971.

and precipitation can be illustrated from a set of samples taken during a storm runoff event in late November 1971 (fig. 7). The rapid initial rise of organic nitrogen concentration can be attributed to flushing of available sources within the vegetation, soil, and atmosphere. The concentration declined as sources within the system were depleted and streamflow rose by about one order of magnitude to peak flow. The concentration rapidly declined on the recession curve to values slightly larger than the mean concentration in precipitation.

Calcium

Calcium outflow closely followed the runoff cycle (fig. 4). The twofold to threefold increase in concentration from winter to the warm seasons had only minimal control on calcium outflow compared with the hundredfold variation in annual runoff. The abrupt concentration drop in late November and the rise in May corresponds approximately to the time that the soil reaches field capacity in the winter and falls below field capacity in the spring (fig. 1).

The calcium and bicarbonate carbon content of the streamflow follow a similar pattern (fig. 8). Winter season values were nearly constant whereas warm season stream contents rose sharply for streamflow values less than $0.1 \text{ m}^3/\text{km}^2\text{-sec}$. The change in slope (fig. 8) corresponds approximately to the change in streamflow regimes (fig. 4) and the time that soil water content rises to field capacity in the winter and departs from it in summer (fig. 1).

Silica

The occurrence of minimum silica concentration in the dry and warm seasons of the year and maxima in the winter and early spring (fig. 5) strongly contrasts calcium concentration-time trends (fig. 4). The silica concentration increase in December and January corresponds to the time of expected recharge of the soil to field capacity. The continued elevation of silica concentration through the winter season suggests that soluble silica is either released by weathering

processes at that time or that it accumulated during the warm season of the year and is removed when wetting fronts flush the soil mantle in midwinter. The reduction of concentration in late April corresponds to the time that subsoils drain as the forest responds to evaporative demand and precipitation lessens.

Discussion

Organic nitrogen has seldom been identified in precipitation. Tarrant et al. (1968) found values of nitrogen input (1.49 kg/ha-yr) similar to those reported here (table 1) and in the same proportions of organic to nitrate nitrogen (87 and 13 percent, respectively). Organic nitrogen from 0.02 to 0.20 mg/l was also found in New Zealand snows by Wilson (1959). Only trace amounts of ammonium were found in the present study and in that by Tarrant et al. (1968). However, Moodie (1964) reported from 1 to 6 kg/ha-yr of ammonium nitrogen at several agricultural sites in western Washington. Values of input for cations, sodium, potassium, calcium, and magnesium (table 1) were generally similar to those reported by Moodie.

Atmospheric particulate matter may contribute substantially to nitrogen and phosphorus input. A large proportion of this is undoubtedly of local terrestrial origin during the dry season and arises from road dust, pollen, and smoke particles. From November through March, when the local environment is regularly dampened by precipitation, particulate matter is thought to be carried from the Pacific Ocean in prevailing westerly winds. Presumably, the finest particles pass the filters we use to separate solids from water and contribute to the "dissolved nutrients." Nearly all the phosphorus and 72 percent of the nitrogen resulted from a digestion of substances in rainwater collected during the dry seasons (table 1).

This forest system retains nitrogen very effectively. The net gain of 0.5 kg/ha (table 2) is nearly equal to that reported by Cole et al. (1967). The fact that this result was duplicated on two Douglas-fir stands, very diverse

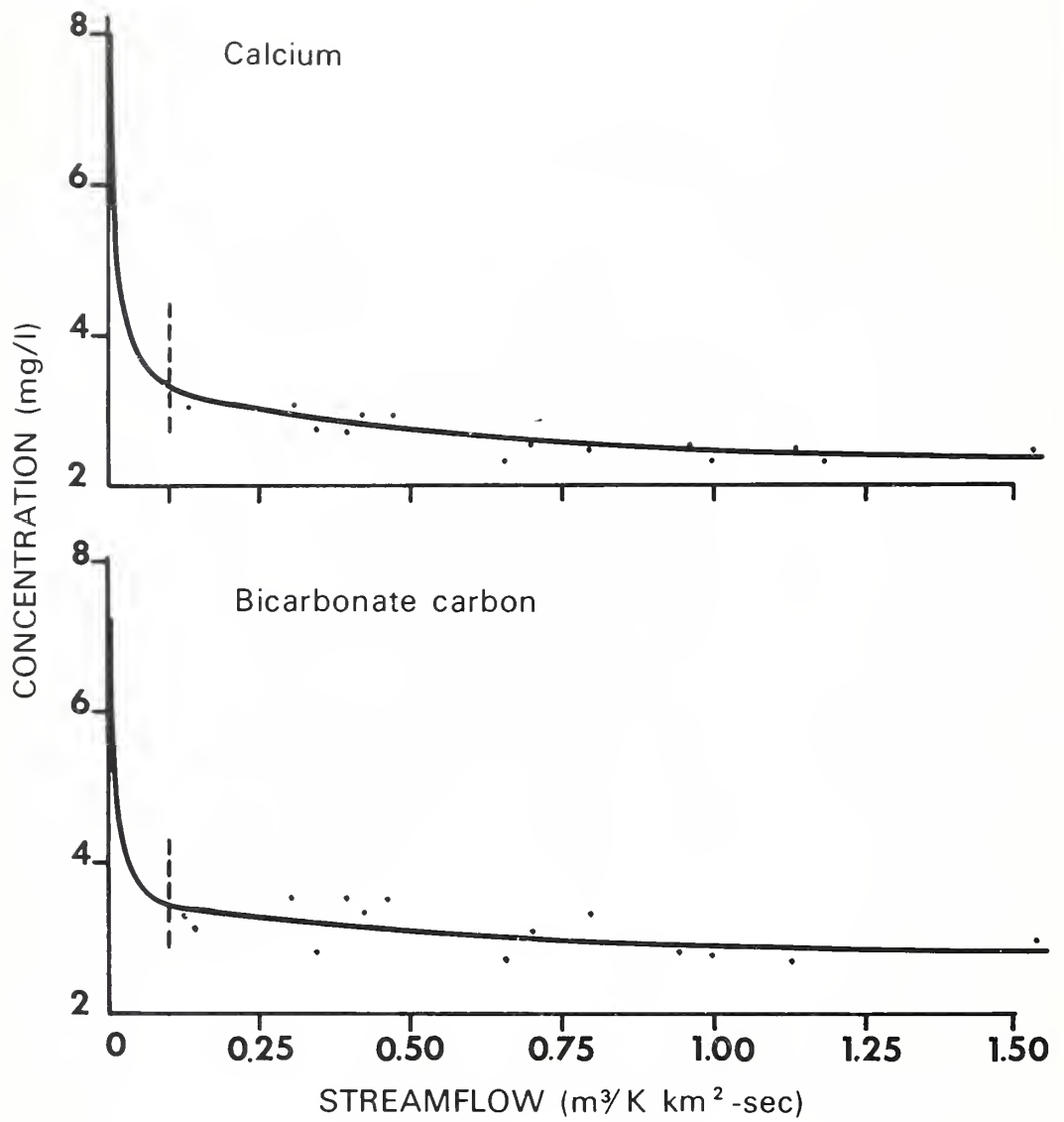


Figure 8. Concentration of calcium and alkalinity as bicarbonate carbon in streamflow, 1970-72.

in terms of soil and stand structure, suggests that this retention property may be general for Douglas-fir forests west of the Cascade Range in the Northwestern United States. Although an explanation for this retention must await the completion of research now in progress, it appears from the small organic nitrogen outflow that most of the soluble organic substances released from decomposition of detritus and organism excretions are rapidly incorporated by the organisms of the forest. Nitrate nitrogen outflow is also regulated to levels much less than the input in precipitation. Either nitrification rates are very low in the soils or the nitrate is retained and rapidly incorporated by the forest system. Nitrification is active in the acid soils of conifer forests on the Oregon coast (Bollen and Lu 1968), but this information is lacking for soils of the H. J. Andrews Experimental Forest.

The status of nitrogen capital of a Douglas-fir forest is the result of a number of processes including input in precipitation, fixation by free living organisms such as blue-green algae and soil bacteria, and fixation by microorganisms living in symbiotic association with a host plant. If the forest gains 0.5 kg/ha annually, as is indicated by this short period of record, 8,000 years would be required to accumulate the 4,000 kg/ha of organic nitrogen found in the more fertile soils of the study watershed. Additions of nitrogen symbiotically fixed by *Ceanothus velutinus* may be somewhat larger. If *Ceanothus velutinus* stands persist for 20 years and fix 20 kg/ha annually as Zavitkovski and Newton (1968) suggest, and if generations of these brush stands are induced by fire at intervals of 200 years, then 16,000 kg/ha of nitrogen would accumulate in 8,000 years. From this, deductions must be made for losses by soil erosion and microbial and fire volatilization. In any case, inputs of nitrogen in precipitation must be considered of importance compared with other mechanisms of gain and loss by the forest.

Phosphorus outflow from the forest was similar to that of nitrogen (table 2). Loss occurs as both organic phosphorus and orthophosphorus. The organic form predominates

in the warm seasons of the year when there is a rapid biological turnover of phosphorus by the forest. Concentration of the ortho form remains fairly constant throughout the year and is thought to arise from mineral weathering.

The losses of the cations sodium, potassium, calcium, and magnesium were large compared with those of nitrogen and phosphorus and represent excess amounts of these cations to the annual requirements of the forest vegetation (table 2). These losses are approximately four times those reported for the Hubbard Brook ecosystem in New Hampshire except for the potassium values which were nearly equal to those reported here (Likens et al. 1970). Cole et al. (1967) also reported lower losses of potassium and calcium. The cation and silica losses (table 2) are estimates of the annual release of these chemicals by mineral weathering. In this regard, it is interesting to note that the ratio of Si:Ca:Na:Mg weathering rates for 1970 are 8.9:4.3:2.1:1.

Another mechanism for nutrient loss is the particulate matter that is transported by the stream. This material may arise from soil erosion or from organic detritus from the forest. Losses of suspended sediment from this study (67 and 37 kg/ha-yr) were much lower than the 12-year annual average of 133 kg/ha from another undisturbed watershed in the Experimental Forest (Fredriksen 1970). Although we have not quantified the chemical loss by this means in this study, previously published annual losses of 0.16 kg/ha for organic nitrogen represent less than half of the dissolved component loss (table 2), still an important part of the total nitrogen loss (Fredriksen 1971). Cation loss was much less than 1 percent of the loss in dissolved form. However, since erosion losses are very sporadic and dependent on extremes of storm runoff events, and the results (Fredriksen 1971) are indicative of the chemical loss during a relatively quiescent period, they should be taken as minimum estimates of nutrient loss by soil erosion processes.

Biological and chemical processes of the forest that control nutrient mobilization and retention are undoubtedly closely linked to environmental factors. The movement of

water is dominant because flowing water is required to transport materials to the sites of physical-chemical and biochemical activity and to remove byproducts that appear in the outflow of experimental watersheds.

Definite concentration changes in the stream occur at the transition periods from drying to wetting of the forest system (figs. 3, 4, and 5). A key feature is either retention of precipitation (and reaction byproducts) in soil storage or the passage of wetting fronts through the soil mantle when the soils are at field capacity. It is not surprising that, of the annual totals, 77 percent of the calcium, 80 percent of the organic nitrogen, and 83 percent of the silica were exported from the forest in the 5 months from December 1969 through April 1970. During this period, the soil mantle was at field capacity and wetting fronts from winter rainstorms regularly flushed the entire forest system.

For organic nitrogen (fig. 3), the period of maximum outflow corresponds to the time when wetting fronts begin to pass through the soil mantle in early December. The widening margin between input and outflow (fig. 6) indicates an increasing contribution to outflow of organic nitrogen from the forest system. Although we do not know how much organic nitrogen from precipitation directly supplements streamflow, the increased concentration and content in precipitation and streamflow in late January suggest that sources of organic nitrogen in precipitation may directly augment the outflow from this experimental catchment.

There is a definite change in the calcium content of streamflow as the hydrologic state of the forest system changes from winter to summer (fig. 8). The calcium outflow was closely paralleled by the content of carbonate and bicarbonate—the predominant anions of the stream. McColl and Cole (1968) demonstrated that cation mobilization is effectively controlled by these mobile anions that are formed by the carbonation of water with carbon dioxide released by respiring organisms of the forest. As yet, we cannot explain the processes that maintain a nearly constant concentration of calcium and these mobile anions over the range of winter streamflow.

Silica is nearly absent in precipitation and is therefore entirely generated within the soil-forest system (fig. 5). Although the parent materials of soil are the primary source of silica, silica is cycled in generous amounts by forests as indicated by litterfall studies (Remezov et al. 1955) and the occurrence of plant opal crystals in forest soils (Paeth 1970). Silica in streamflow may originate from primary mineral weathering, secondary mineral dissolution, or release from decomposition of detritus. Silica may be taken out of solution by formation of secondary minerals within the soil. The occurrence of minimum silica concentration in the dry and warm seasons of the year and maxima in the winter and early spring strongly contrasts calcium concentration-time trends (fig. 4).

Acknowledgments

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Nutrient cycling in throughfall and litterfall in 450-year-old Douglas-fir stands

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Abstract

*Comparisons of nutrient concentrations (N, P, K⁺, Ca⁺⁺, Mg⁺⁺) found in canopy throughfall and litterfall were made on the H. J. Andrews Experimental Forest. Six old-growth Douglas-fir (*Pseudotsuga menziesii*) stands were studied which represented six forest communities common to the western Cascades of Oregon. These community types span a large portion of the temperature and moisture gradients present in the area. The preliminary data indicate that nutrient concentration in throughfall was highest during the summer and fall, and lowest during the winter. Nutrient input through throughfall generally followed the same trends. Nutrient return through litterfall was greatest in the needles. More amounts of N, P, and Ca⁺⁺ were transferred to the soil through litterfall than through throughfall, while more K⁺ and Mg⁺⁺ were added to the soil through throughfall. Litterfall was maximum during the winter. Future studies will correlate the results from the nutrient analysis to the moisture and temperature gradients.*

Introduction

The worldwide interest of scientists in litterfall production during the past century, has been shown by Bray and Gorham (1964) in their review of litter production in the forests of the world. Methodology reports ranged from utilization of randomly located collection devices of varied design, separation, oven-drying, and chemical analysis of several litter components, to merely raking up and air drying the litter on a unit area basis. In spite of the large number of papers cited in the above review, data of litter production from natural, old-growth ecosystems are meager. Even less is known about litterfall in old-growth Douglas-fir (*Pseudotsuga menziesii*) forest types. The examination of seasonal fluctuations, nutrient concentration changes associated with defoliation, and nutrient composition of various litterfall categories are scarce

(Kira and Shidei 1967).

The first published report of an investigation of litterfall in coniferous forests of the Pacific Northwest is that of Tarrant, Isaac, and Chandler (1951). These workers collected the litter of several species for 1 year and estimated nutrient movement by multiplying litter weight by the percent elemental content of foliage collected from trees, an inexact procedure. More detailed measurements of the nutrient cycle in Douglas-fir forests have been published for stands in New Zealand (Will 1959) and the United States (Dimock 1958). In addition, workers at both the University of Washington (Rahman 1964) and Oregon State University¹ have collected substantial data describing litterfall in both managed and natural Douglas-fir stands. Riekerk and Gessel (1965) and Cole and Gessel (1968) summarize

¹ D. P. Lavender, unpublished data.

a number of very sophisticated studies of nutrient movement through Douglas-fir ecosystems in Washington.

All of the above studies, save that of Tarrant et al., however, were concerned with litterfall and nutrient movement through relatively young stands.

Several studies (LeClerc and Breazeale 1908, Mes 1954, Tukey and Amling 1958, and Tukey et al. 1958) have demonstrated that rainfall may remove substantial quantities of nutrient elements from the foliage of horticultural plants. Similarly, studies of the elemental content of precipitation under forest stands (Tamm 1951, Madgwick and Ovington 1959, Will 1959, and Voigt 1960) have demonstrated that rainwater which has passed through tree crowns ("throughfall") contains significantly higher quantities of many nutrient elements than rainfall collected in adjacent openings.

In the Pacific Northwest, studies reported by Rahman (1964), Tarrant et al. (1968) and Cole and Gessel (1968) have yielded data which describe the movement of nutrients from the atmosphere and tree crowns to the forest floor by precipitation. Finally, unpublished data by Lavender describe the movement of nutrients from the crowns of both fertilized and control second-growth Douglas-fir stands to the forest floor by precipitation.

The purpose of the present study was to measure the movement of nutrients in canopy throughfall and litterfall in several association types of old-growth Douglas-fir stands. These community types were selected to represent the range of environments occurring on the H. J. Andrews Experimental Forest and are also indigenous to the Pacific Northwest. This paper will report on the results of our efforts to date.

Study Area

The H. J. Andrews Experimental Forest encompasses 15,000 acres and is characterized by steep topography with approximately one-fifth of its land area in gentle slopes or benches. Elevations within the forest vary

from 457 m to more than 1,523 m. Precipitation is heavy, varying from 226 cm per year at lower elevations to as much as 356 cm per year along the highest ridges. A considerable snow-pack develops on the higher slopes while rain predominates at the lower elevations. Mean temperatures within the forest range from 35°F in January to 65°F in midsummer (Berntsen and Rothacher 1959).

Methods

Within the Experimental Forest, six communities were chosen (table 1), each named for characteristic plants in both the overstory and understory. The six old-growth communities are presented in order of increasing elevation. Each of the six plots are 0.2024 hectare in size and are equipped with eight litter traps; each is 2,601 cm² in area, located on a random basis in each plot. Litter was collected every 4 to 6 weeks during the snow-free months of 1970-71. Heavy snow pack prevented litter collection during much of the winter of 1970. Therefore, data describing nutrient movement in the litter for this period are weak because: (1) the necessarily infrequent collections do not permit accurate assessment of the rate of litterfall, and (2) litter which remained in the traps for long periods was subjected to leaching. The following fall, three litter traps on each plot were equipped with a 113-liter reservoir to collect the precipitation which passed over the litter. Analysis of this water will provide a measure of the nutrients leached from the litter. Crown and stem maps were made for each plot to aid in evaluating the variation of litterfall between traps.

After collection the litter for each trap was dried at 70°C, separated into classes (needles, cones, twigs, branches, hardwoods, bark, lichens and mosses), and weighed. Prior to chemical analyses, litter from the eight litter traps per plot was composited into two samples, each representing four traps. In addition, some consolidation of litter collected on different dates was necessary. Each sample was analyzed to determine the levels of nitrogen, phosphorus, potassium, calcium and

Table 1.—Characteristics of study plots

Plot	Elevation	PPT/ year	Percent species composition ¹		Diameter range	Average d.b.h.	Basal area ²	Stems/ hectare
	meters	centimeters			--- centimeters ---			
1. <i>Pseudotsuga- Holodiscus</i>	457	211.8	Psme	89.3	11 — 163	46.7	83.06	277
			Tsme	5.4				
			Tabr	3.6				
			Acci	1.7				
2. <i>Tsuga- Rhododendron- Berberis</i>	488	228.3	Psme	17.0	8 — 139	37.8	97.55	494
			Tsme	69.0				
			Tabr	8.0				
			Thpl	5.0				
			Conu	1.0				
3. <i>Tsuga- Polystichum</i>	762	230.6	Psme	26.5	10 — 213	68.1	120.87	168
			Tsme	61.8				
			Tabr	8.8				
			Thpl	2.9				
4. <i>Tsuga- Rhododendron- Gaultheria</i>	610	229.6	Psme	52.8	8 — 157	34.0	69.77	450
			Tsme	23.1				
			Tabr	1.1				
			Thpl	19.8				
			Cach	2.2				
			Conu	1.1				
5. <i>Tsuga-Abies- Linneae</i>	975	—	Psme	16.1	8 — 173	66.3	129.60	277
			Tsme	46.4				
			Thpl	33.9				
			Tabr	3.6				
6. <i>Abies- Tiarella</i>	1,311	—	Psme	46.3	8 — 117	55.4	109.63	331
			Tsme	16.4				
			Abam	37.3				
			Abpr					

¹ Psme *Pseudotsuga menziesii*
Tsme *Tsuga mertensiana*
Tabr *Taxus brevifolia*
Acci *Acer circinatum*
Thpl *Thuja plicata*
Conu *Cornus nutallii*
Cach *Castanopsis chrysophylla*
Abam *Abies amabilis*
Abpr *Abies procera*

² Square meters/hectare.

magnesium.

In addition to the litter traps, each plot was equipped with four 20-inch-high rain gages. Each gage was assigned to one of 20 random locations within the plot after each collection, in accordance with a method described by Wilm (1943). Higher elevation plots also contain a rain gage on a platform 10 feet from ground level to provide a water sample during months of heavy snow cover. Water was collected and the volume measured at approximately 2-week intervals. The samples were returned to the laboratory on the day of collection, filtered, and stored at -12°C until thawed for analysis. For analysis, the four samples per plot were combined into two samples and analyzed for total potassium, calcium, magnesium, orthophosphate, and total phosphorus. Nitrogen in the form of ammonium, nitrate, nitrite, and organic nitrogen was also determined.

Precautions were taken to keep contamination of water samples to a minimum. Funnels with glass wool stoppers were provided for each rain gage to keep organic matter from contaminating water samples. Mercuric chloride was added to the rain gages in the summer and fall to keep microorganism activity to a minimum. The cold temperature helped to reduce microorganism and insect activity during the winter.

Several techniques were investigated in an effort to arrive at a measure of crown density. Basal area and volume poorly describe intercepting crown cover in old-growth defective stands as canopy development tends to remain constant after trees reach maturity; hence, direct estimates were used. Photographs which were taken above each sampling point with a 35-mm camera were shown over a spherical dot grid to give a means of comparing crown densities.

Results and Discussion

Throughfall Results

Nutrient concentration in throughfall samples for plots 1 through 4 for all elements appeared to be the same during each season

(fig. 1). Water sample concentrations were highest during the summer when precipitation was minimal (table 2). Concentrations were lowest during the winter when precipitation was highest. As precipitation decreased from winter to spring, concentration of throughfall samples for each element increased. Throughfall concentrations were also high during the fall when precipitation first starts.

Unlike N, the average total input of P, Mg^{++} , Ca^{++} , and K^{+} generally follows the same trend as did the concentration curves (fig. 2). The greatest amount of each element was leached out during the fall when precipitation first washes the canopy. Decreasing amounts were leached out with increasing precipitation. Potassium input reached a low point during the winter, at which time 68 percent of the total precipitation had fallen, and

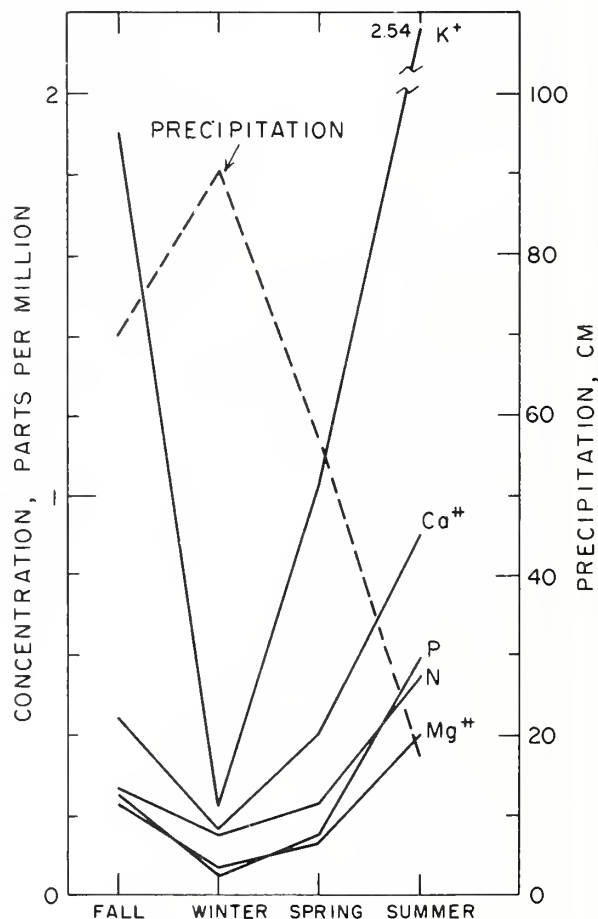


Figure 1. Average concentration of plots 1 through 4 for each element by season.

Table 2.—Average total precipitation across all plots by season

Season	Precipitation
	centimeters
Fall	70.89
Winter	92.05
Spring	57.96
Summer	18.08
Total	238.98

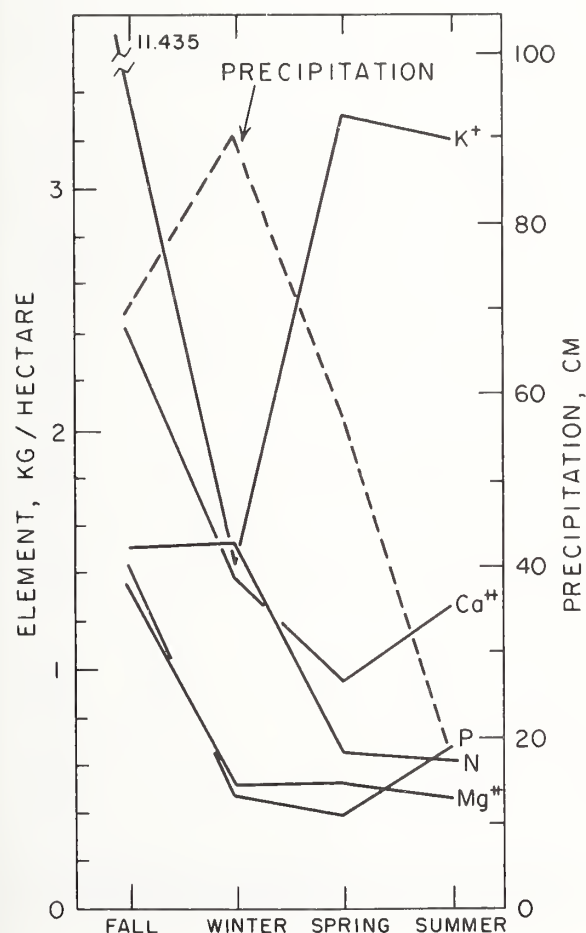


Figure 2. Total average kg per hectare of plots 1 through 4 for each element by season.

increased sharply from winter to spring, slightly decreasing from spring to summer. Calcium and P reached low points during the spring, at which time 92 percent of the total precipitation had fallen, and increased from spring to summer. Magnesium input was greatest from fall to winter and remained approximately the same from winter to summer. Nitrogen input slightly increased from fall to winter, decreasing from winter to spring reaching a low point during the summer.

There appears to be no difference in terms of net kg per hectare per year between plots 1 to 4 for each element with the exception of plot 3 (table 3). Plot 3 had more K⁺ and less Ca⁺⁺ than plots 1, 2, and 4.

Throughfall Discussion

In general, the total nutrient input and throughfall concentrations were highest in the summer and fall and lowest during the winter and spring months. This seems to indicate that each tree or canopy has a constant fraction of elements which can be removed from the foliage through leaching elements. Once the rains start in the fall, the majority of each nutrient is leached out. As the rains increase in quantity and duration during the winter and spring months, the available fraction of nutrients is further depleted. Decreasing precipitation from spring to the end of summer allows the nutrient fraction to increase again until the total fraction of leachable nutrients is reached.

Variations found between plot 3 and plots 1, 2, and 4 with respect to K⁺ and Ca⁺⁺ could be due to differences in soil types (data not available yet). If soil types are different with respect to nutrient availability, the differences between plots could be explained by luxury consumption.

Another possible source of the nitrogen found in the throughfall samples is nitrogen-fixing bacteria. Jones (1970) in his study of nitrogen fixation by bacteria in the phyllosphere of Douglas-fir (*Pseudotsuga douglasii*) in England isolated bacteria from the leaf surfaces of Douglas-fir. He found that the bacteria could fix atmospheric nitrogen when provided with a carbohydrate source. The fate

Table 3.—Net kg per hectare per year of nutrients collected in throughfall gages

Item	N	P	K ⁺	Ca ⁺⁺	Mg ⁺⁺
Input from atmosphere ¹	1.298	0.232	0.106	2.085	1.273
Throughfall input:					
Plot 1	3.999	2.308	17.416	5.983	2.608
2	2.979	2.398	15.749	4.438	2.086
3	3.729	2.970	30.350	2.134	1.456
4	2.710	3.283	23.379	5.104	2.343
Average	3.354	2.740	21.724	4.416	2.123

¹ Fredriksen unpublished data—data collected from open area on the H. J. Andrews Experimental Forest at 610 meters.

Table 4.—Distribution of metric tons/hectare between litter components by plot

Plot	1	2	3	4	5a	5b ¹	6	Average ²
Needles	2.002	2.246	2.950	3.200	2.533	2.533	3.741	2.777
Percent of total	32.84	35.56	46.44	62.30	15.17	55.91	54.10	47.15
Reproductive structures	.834	1.141	1.284	.742	.536	.536	.518	.743
Percent of total	13.68	18.06	20.22	14.46	3.20	11.83	7.49	14.31
Wood material	2.280	2.760	1.876	1.009	13.479	1.267	2.524	1.953
Percent of total	37.40	43.68	29.53	19.66	80.74	27.96	36.50	33.14
Hardwoods and mosses	1.022	.175	.401	.197	.195	.195	.206	.365
Percent of total	16.77	2.77	6.32	3.84	1.17	4.30	2.98	6.20
Total	6.138	6.317	6.512	5.131	16.694	4.530	6.916	5.891

Note: In plot 5, an extremely large slab of bark from a nearby snag fell into a trap causing high values for total tons/hectare. Over a longer period of time, this type of variation between litter components can be expected to occur randomly throughout each plot. However, due to the limited sampling time thus far recorded, the one extreme value will be temporarily ignored.

¹ Excluding extreme bark sample.

² Excluding 5a.

of the nitrogen was not determined. However, Jones suggested that it could be washed to the ground.

Litterfall Data

Despite the differences in stand characteristics shown in table 1, little variation in total litter production was found among stands for the year 1970-71 (table 4). Average yearly litterfall production for all plots was 5.89 metric tons/hectare. This is approximately 1½ times the average 3.5 metric tons per hectare reported by Bray and Gorham (1964) for cool, temperate forests, but closer to the yield they reported for a latitude comparable to their study area (fig. 1). From worldwide data, these authors reported that nonleaf litter averaged from 27 percent to 31 percent of total litter production. The stands reported here averaged 47 percent nonleaf (woody) litter for the 1-year period.

In terms of total kg/hectare of litter, the vast majority fell during the winter (fig. 3). This is the period when snowfall is greatest, consequently much litter breaks under the

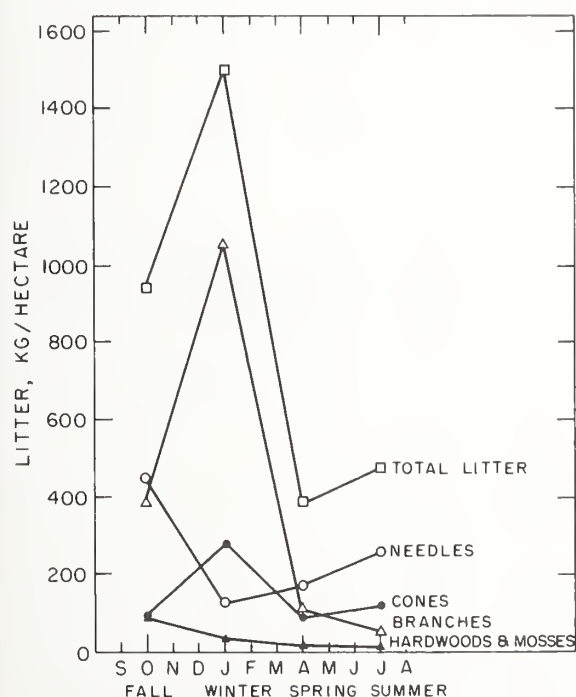


Figure 3. Average kg per hectare by season and litter component.

weight of the snow. Needle cast was greatest in the fall, decreasing during the winter, and gradually increasing during spring. Hardwood and moss litter was greatest in the fall, decreasing throughout the rest of the year. Woody material and cone litterfall was greatest during the winter.

Nutrient concentration of litterfall components varied considerably among plots and seasons (table 5). Plots 1 and 3 were chosen to represent the range of values that can be found in nutrient return through litterfall. There appears to be no consistent trend by season or plot for the litter component concentrations. However, average yearly concentrations of each nutrient for each litter class are comparable between plots 1 and 3. There is a substantial difference between total kg/hectare for N, P, K⁺, and Ca⁺⁺ between plots (table 6). Plot 1 had more kg of Ca⁺⁺ per hectare than did plot 3. Plot 3 had greater amounts of N, P, and K⁺ than did plot 1. Little difference occurred among plots for Mg⁺⁺.

The greatest portion of nutrient input through litterfall came in the needles (table 7). Needle litterfall contributed about 54 percent of the total nutrient input. Cone litterfall accounted for 13 percent while twig litterfall accounted for 11 percent of the total. Together, the needle, cone, and twig litterfall account for 78 percent of the total nutrient input through litterfall.

Litterfall Discussion

Variations in nutrient concentration found between litterfall components among plots and season can be expected if foliage characteristics such as age and species are not constant. We also observed that the age of the tissue, and when it falls, varies throughout the year for each plot. This is primarily due to environmental parameters such as wind action, rainstorms, and snowfall. Differences in soil types could also have affected concentrations.

Differences between total nutrient input through litterfall (table 6) are affected by the distribution of litter components within the total. Where two plots seem to produce com-

Table 5.—Average percent of N, P, K⁺, Ca⁺⁺, and Mg⁺⁺ by season, plot, and litter component

Litter component and season	Plot 1					Plot 3				
	N	P	K ⁺	Ca ⁺⁺	Mg ⁺⁺	N	P	K ⁺	Ca ⁺⁺	Mg ⁺⁺
Needles:										
Fall	0.368	0.087	0.109	1.901	0.017	0.434	0.120	0.161	1.815	0.020
Winter	.691	.108	.210	1.305	.018	.763	.124	.280	1.103	.081
Spring	.462	.124	.159	1.241	.028	.717	.119	.103	1.112	.017
Summer	.467	.143	.200	1.740	.034	.474	.105	.145	1.286	.025
Average	.497	.115	.169	1.546	.024	.597	.117	.172	1.329	.020
Cones:										
Fall	.530	.084	.122	.397	.045	.518	.063	.099	.149	.015
Winter	.294	.029	.046	.146	.016	.387	.033	.051	.148	.011
Spring	.488	.049	.133	.214	.041	.544	.064	.102	.178	.011
Summer	.487	.068	.151	.369	.027	.561	.063	.159	.206	.016
Average	.449	.057	.105	.281	.032	.502	.055	.103	.170	.013
Twigs:										
Fall	.340	.033	.051	.852	.009	.434	.051	.124	1.107	.016
Winter	.375	.040	.057	1.261	.011	.398	.032	.075	1.110	.012
Spring	.424	.072	.076	.999	.081	.358	.047	.046	.823	.008
Summer	.408	.043	.105	1.034	.013	.363	.055	.102	1.054	.015
Average	.386	.047	.072	1.036	.013	.388	.046	.086	1.023	.013
Branches:										
Fall	.218	.017	.030	.713	.008	.207	.013	.025	.522	.006
Winter	.028	.017	.080	.598	.006	.296	.039	.082	.843	.010
Spring	—	—	—	—	—	—	—	—	—	—
Summer	—	—	—	—	—	.102	.008	.030	.338	.005
Average	.213	.017	.055	.655	.007	.201	.020	.046	.567	.007
Bark:										
Fall	.332	.047	.076	.566	.014	.417	.038	.074	.517	.010
Winter	.404	.033	.050	.963	.010	.431	.035	.057	.413	.009
Spring	—	—	—	—	—	.476	.080	.055	.300	.009
Summer	.320	.030	.051	.637	.011	.541	.056	.163	.474	.012
Average	.352	.036	.059	.722	.011	.466	.052	.087	.426	.010
Hardwoods:										
Fall	.630	.095	.167	2.395	.037	.591	.124	.475	2.428	.061
Winter	—	—	—	—	—	—	—	—	—	—
Spring	—	—	—	—	—	—	—	—	—	—
Summer	.546	.092	.302	2.127	.070	—	—	—	—	—
Average	.588	.094	.234	2.261	.053	.591	.124	.475	2.428	.061
Mosses and lichens:										
Fall	.417	.053	.117	.408	.016	.659	.126	.229	.413	.019
Winter	1.264	.100	.132	.567	.015	1.234	.122	.350	.329	.017
Spring	—	—	—	—	—	—	—	—	—	—
Summer	1.313	.100	.246	.376	.020	1.427	.130	.284	.364	.018
Average	.998	.084	.165	.450	.017	1.106	.126	.287	.368	.018

Table 6.—Total kg per hectare per year for plots 1 and 3 for each element by litter class

Litter class	Plot 1					Plot 3				
	N	P	K ⁺	Ca ⁺⁺	Mg ⁺⁺	N	P	K ⁺	Ca ⁺⁺	Mg ⁺⁺
Needles	7.93	2.27	3.16	35.89	0.47	15.61	3.82	5.89	44.08	0.65
Percent of total	36.12	58.85	49.54	50.22	44.61	47.76	68.20	60.25	69.90	59.79
Cones	3.46	.45	.83	2.06	2.13	6.60	.69	1.33	2.05	.17
Percent of total	15.74	11.59	13.03	2.89	20.31	20.23	12.40	13.63	3.24	15.46
Branches	1.97	.16	.74	5.09	.06	.82	.12	.29	2.15	.02
Percent of total	8.98	4.06	11.56	7.13	5.28	2.50	2.00	2.97	3.40	2.06
Twigs	3.52	.38	.66	12.01	.10	3.54	.34	.75	9.56	.10
Percent of total	16.07	9.86	10.33	16.79	9.50	10.82	6.20	7.67	15.15	9.27
Bark	1.62	.11	.07	3.56	.30	3.00	.28	.49	3.18	.06
Percent of total	7.39	3.17	3.08	4.97	2.92	9.18	5.00	5.04	5.03	5.15
Hardwoods	2.33	.39	.67	12.48	.17	.38	.06	.11	1.51	.05
Percent of total	10.60	9.17	10.49	17.46	16.06	1.16	1.00	1.14	2.39	4.12
Moss and lichens	1.12	.08	.12	.39	.01	2.73	.28	.90	.54	.03
Percent of total	5.10	2.11	1.98	.54	1.32	8.35	5.00	9.16	.85	3.09
Total	21.95	3.86	6.39	71.49	1.07	32.68	5.59	9.77	63.06	1.09

Table 7.—Average percent of litterfall totals for plots 1 and 3 for each element by litter class

Litter class	N	P	K ⁺	Ca ⁺⁺	Mg ⁺⁺	Average
Needles	41.9	63.5	54.9	60.1	52.2	54.52
Cones	18.0	12.0	13.3	3.1	17.9	12.86
Branches	5.7	3.0	7.3	5.3	3.7	5.00
Twigs	13.4	8.0	9.0	16.0	9.4	11.16
Bark	8.3	4.1	4.1	5.0	4.0	5.10
Hardwoods	5.9	5.1	5.8	9.9	10.1	7.36
Moss and lichens	6.7	3.6	5.6	.7	2.2	3.76

parable total quantities of litter on a yearly basis, amounts of the various litter components are important. The amounts of each litter component are important because concentrations of nutrient elements vary for each litter component (see table 5). Table 4 shows that the greatest differences between plots 1 and 3 in terms of kg/hectare of litterfall occur between needles and woody material. Plot 3 produced 947 kg/hectare more of needles than plot 1, while plot 1 produced 403 kg/hectare more of woody material than plot 3. However, table 5 shows that the average concentration of nitrogen, for example, is much higher in needles than it is in woody material; consequently, variations such as found in table 6 are brought about.

Nutrient input in both throughfall and litterfall appears to have the same trend for K^+ , P, and Ca^{++} when comparing plots 1 and 3. The litterfall analysis shows plot 3 having more K^+ , P, and less Ca^{++} than plot 1. The throughfall data for plots 1 and 3 show the same results (table 3). However, differences between N and Mg^{++} input through throughfall and litterfall for each plot do not agree. Table 3 shows little difference in N input for each plot, while table 6 shows N being higher in plot 3. A possible explanation for this has been given in the preceding paragraph. Table 3 shows that plot 1 had more Mg^{++} input than plot 3. Litterfall input for Mg^{++} was about the same between plot 1 and 3. A possible explanation for the difference between plots 1 and 3 for Mg^{++} in throughfall might be that the hardwood litterfall accounted for 10.1 percent of the total Mg^{++} input (table 7). Table 1 shows that 1.7 per-

cent of the species composition in plot 1 was hardwoods, while plot 3 shows no hardwoods.

More amounts of N, P, and Ca^{++} were transferred to the soil through litterfall than through throughfall; while more K^+ and Mg^{++} were added to the soil through throughfall (table 8).

There appeared to be no relationship between nutrient concentration and elevation. Rather, concentration on each plot seemed to be correlated with crown density. Basal area and crown density in old-growth Douglas-fir stands seem to be distributed randomly over the sites on the H. J. Andrews Experimental Forest. Consequently, no real correlation could be seen between basal area and crown density with moisture and elevation. This could also be due to the fact that the range of environments sampled on the H. J. Andrews Experimental Forest was not great enough, indicated by total precipitation. Table 1 shows that there was no real difference in total precipitation between plots 1 through 4.

Summary

The preliminary data indicate that nutrient concentration in throughfall varied with season. Highest concentrations were found in the summer and lowest concentrations during the winter. Nutrient input through throughfall generally followed the same trends as did nutrient concentrations. Nutrient return through litterfall was greatest in the needles. Together, the needles, twigs, and cones accounted for 78 percent of the nutrient input

Table 8.—Total nutrient input in kg per hectare per year

Input	N	P	K^+	Ca^{++}	Mg^{++}
Average throughfall input	3.3544	2.740	21.7230	4.416	2.123
Average litterfall input	27.3235	4.725	8.0784	67.2738	1.080
Total	30.6779	7.465	29.8014	71.6888	3.203

through litterfall. More amounts of N, P, and Ca^{++} were transferred to the soil through litterfall than through throughfall, while more K^+ and Mg^{++} were added to the soil through throughfall. Litterfall was maximum during the winter.

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*Estimating Biomass
and Other State Variables*

Direct, nondestructive measurement of biomass and structure in living, old-growth Douglas-fir [*tree-climbing techniques*]

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Abstract

Previous studies of biomass and structure of Douglas-fir have examined trees less than 100 years old. This paper describes methods for measuring older trees, illustrated by data from a tree 60 m tall and 450 years old.

Rock climbing techniques, modified for use on trees, are employed to climb the main trunk. A movable spar provides access to lateral branches. The trunk is measured, the position of each branch system is located on it, and the branch systems are scored for 10 variables related to biomass and structure. An importance value, calculated for each branch system, is used in selecting a set of branch systems for detailed measurement. The data permit diagrammatic reconstruction of the tree, or estimates of the distribution or total amount of component parts.

Introduction

The techniques described in this paper are of two kinds; technical climbing methods and methods of tree description and measurement which depend upon technical climbing to provide access to the top of the tree. In combination, these techniques are designed to provide quantitative descriptions of the biomass, surface area, and spatial distribution of the aboveground parts of individual trees.

The climbing techniques developed from a National Science Foundation-Undergraduate Research Participation study of epiphytes on old-growth Douglas-fir (*Pseudotsuga menziesii*). Previous studies (Coleman, Muen-scher, and Charles 1956; Hoffman and Kaz-mierski 1969) were limited to epiphytes

within 2 m of the ground, but this study was designed to study the canopy populations as well. An initial attempt to use felled trees was unsuccessful because the surface of the trunk which hit the ground was destroyed and the branch systems with their epiphytes were shattered and scattered. The climbing techniques were developed as an alternative and proved to be practical, effective, and economical.

Five old-growth Douglas-firs have been rigged and climbed to date, but only one has been subjected to the measurement and analysis described herein. Previous studies of biomass in this species (Burger 1935; Newbold 1967; Reukema 1961) have been limited to trees less than 100 years old, but the trees used in our study are 450 years old and large;

60-80 m tall, 1-1.5-m dbh, with their lowest branches 12-25 m above the ground.

Climbing trees of this height is dangerous. A fall would probably be fatal. But probably there is greater danger of injury to personnel under the tree in the event equipment or parts of branch systems are accidentally dropped upon them. We have worked through two seasons without injury.

The climbing techniques are described in detail to permit others to adopt them. The rock-climbing techniques on which they are based are described in books on mountaineering (Blackshaw 1970; Manning 1967) but may be unfamiliar to biologists.

The access technique, the methods of description and measurement, and one application of the data, a diagrammatic reconstruction of a tree, are treated in this paper. Another paper in this symposium (Pike et al. 1972) describes the estimation of tree surface area and epiphyte biomass.

The Access Techniques

Access to the tree involves three steps: rigging, climbing, and use of the spar, each described below. Rigging and climbing techniques are modified from direct-aid rock-climbing techniques. Basic safety procedures, equipment, terminology, and philosophy have been adopted from mountaineering. Anyone without prior mountaineering experience who expects to adopt these techniques should consult one of the standard texts (Blackshaw 1970; Manning 1967). The specialized rope and hardware may be obtained from either mountaineering or yachting suppliers.

Basic equipment for all climbers includes: hard hat, heavy climbing shoes, and a harness of nylon webbing to which a belay rope is attached. The climber is always belayed—that is, she is protected by a safety rope held by another experienced climber. Climbing and belay ropes are 11 mm nylon “goldline” and the webbing used in making slings, stirrups, etc. is of nylon and 40-50 mm wide.

Rigging

Rigging involves an initial ascent and preparation of the tree for subsequent climbing. The ascent is slow, and requires exceptional agility and endurance. A team of three experienced climbers should rig the tallest trees in a day and a half.

The procedure used in ascending the tree and placing climbing and belay ropes is outlined in figures 1-4.

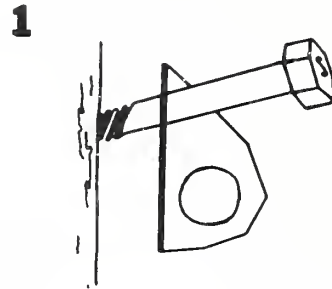


Figure 1. A lag screw is used to fasten a steel hanger to the tree.

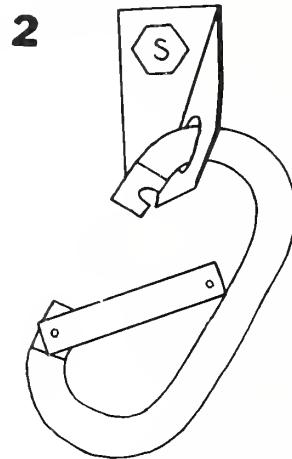


Figure 2. A carabiner is clipped into the hanger.

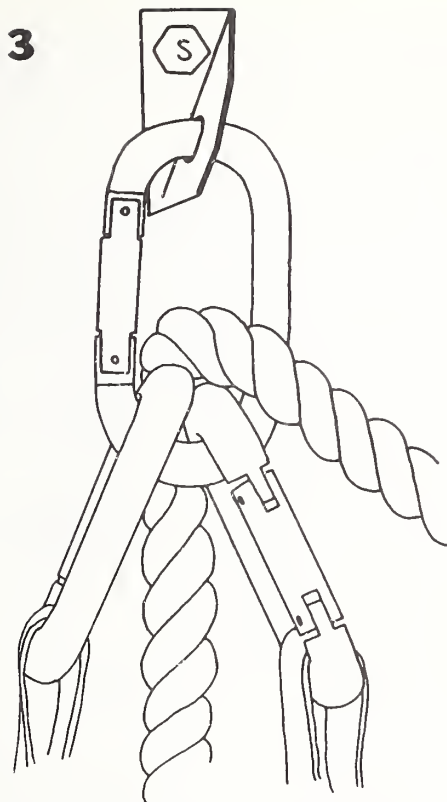


Figure 3. Two additional carabiners are used to fasten two climbing stirrups to the first carabiner. (Only the upper ends of the webbing stirrups are shown.) The belay rope is clipped through the carabiner.

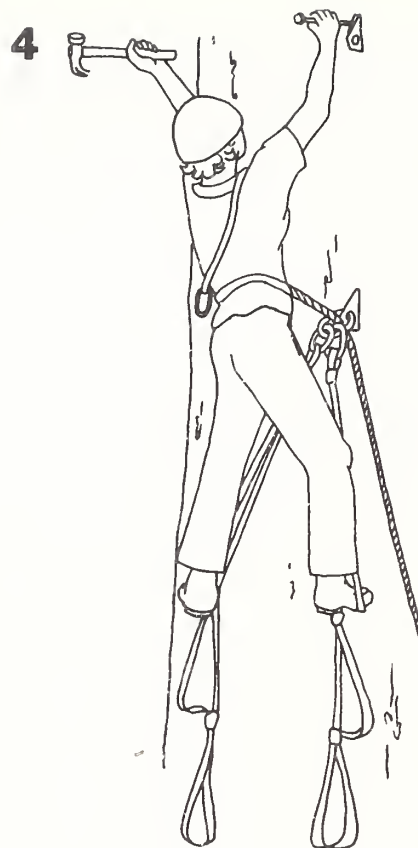


Figure 4. The climber ascends the climbing stirrups until the first carabiner is at her waist. Tension on the belay rope holds her in position while she drives the next lag screw.

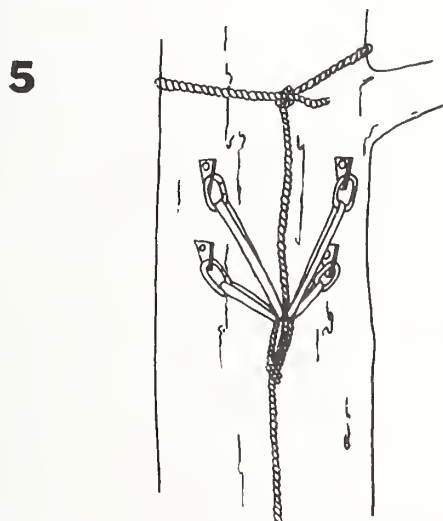


Figure 5. The climbing rope is fastened to the tree by four lag screws, hangers, and carabiners. A loop, tied near the end of the rope, is connected to the carabiners by two loops of webbing. The free end of the rope is tied around the tree using a bowline.

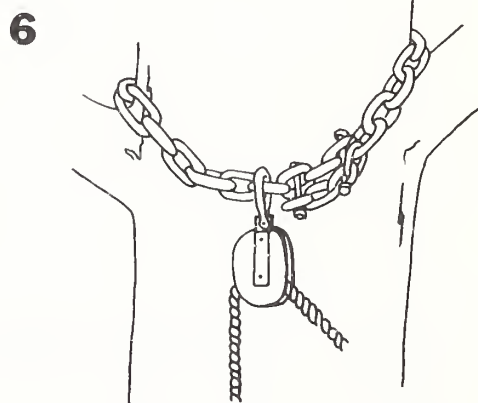


Figure 6. The belay rope runs through a block hung by heavy chain with welded links. The chain is fastened around the tree above a limb and secured by two 1-cm bolts with washers and lock nuts.

Lag screws, 8 by 150 mm, are used to attach equipment. They do not sag or "work out" of the thick, soft bark of Douglas-fir as nails do. The screws are driven with a hammer but may be tightened or removed with a wrench.

A climbing rope is attached near the top of the tree and subsequent ascents are made on this fixed rope. Figure 5 illustrates the usual method of attachment.

The block for the belay line is attached below the point at which the climb path is obstructed by branches. In climbing above this point the belay rope is carried up through carabiners placed during rigging. Below the block, on the open trunk, the climber is belayed from above through the block. Figure 6

illustrates the method of attachment for the block.

Climbing

Climbing requires mastery of unfamiliar skills, but no greater strength or agility than climbing a ladder, a 70-m ladder. An experienced climber, in good physical condition, can climb a 75-m tree in 20 minutes or less, depending upon the distribution of branches and the lean of the trunk. A clumsy, middle-aged man can clamber up with equal safety, but it takes longer.

The techniques involved in climbing the fixed rope are illustrated in figures 7-13.

7

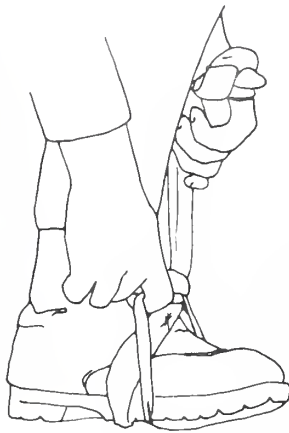


Figure 7. A band of rubber cut from a motorcycle innertube is fastened around the sling and over the toe of the boot to prevent the climber from accidentally stepping out of the sling.

8

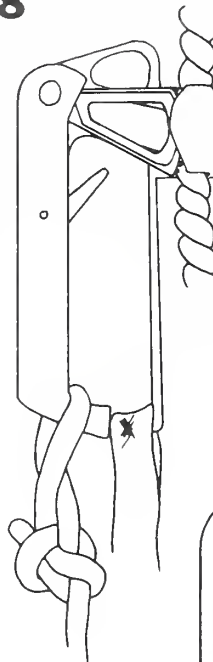


Figure 8. When weight is placed on the jumar, its toothed gate grips the rope so that the jumar can move neither up nor down.

9

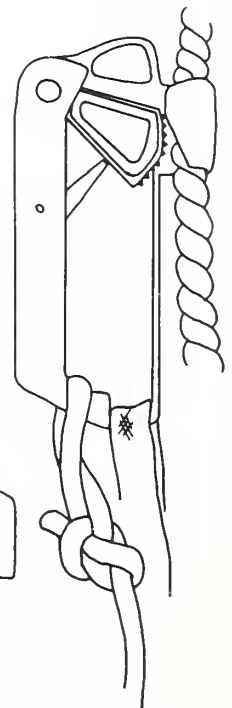


Figure 9. When there is no weight on the jumar, its gate may be lowered and the jumar moved up or down the rope.

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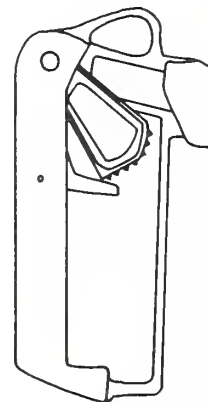
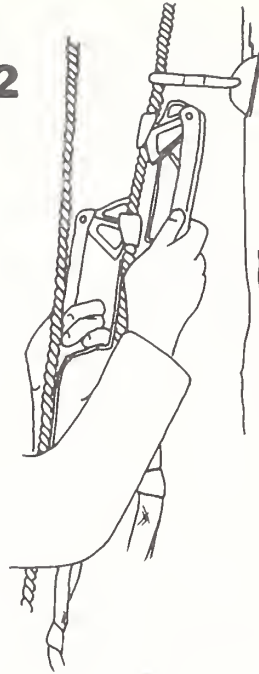


Figure 10. The jumar cannot be removed from the rope unless the safety catch is depressed to permit the gate to open fully.

11



12



13

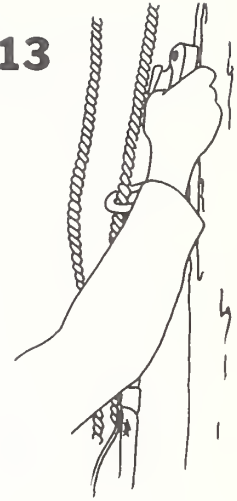


Figure 11. The climber places her weight on one foot, thus locking the jumar on that side, while she moves the other jumar up or down. She ascends or descends by shifting her weight from one foot to the other and moving the opposing jumars. She stands in webbing slings which hang from the jumars. The jumars are connected to each other by a short length of rope which passes through a carabiner clipped to her belay harness.

Figures 12 and 13. At those points at which the climbing rope is fastened by a carabiner, the jumars must be disconnected from the rope, one at a time, and moved around the carabiner.

Most of the carabiners used in rigging are removed once the tree is rigged, but a few are left in place to prevent the climbing rope from hanging away from the trunk.

Shouted instructions from climber to belayer are normally adequate during climbing, but once the climber enters the canopy conversation is severely impeded by distance and intervening foliage. A pair of small radio transceivers facilitates longer communications and permits the belayer to record data dictated by the climber.

The Spar

Use of a special boom, hereafter called "the spar," permits the climber to reach any point within 4 m of the trunk.

The spar is specially constructed of three lengths of mast-grade spruce laminated in a "tee" cross section. It is 4 m long and together with its hardware and rigging it weighs 15 kg. It is awkward to maneuver into place, especially where there are branches close above the one to be sampled. Under normal

14

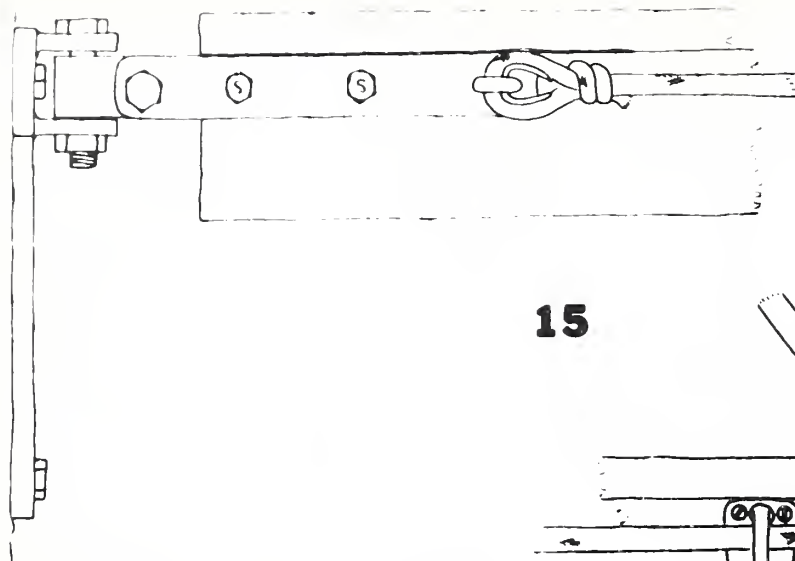


Figure 14. The inboard end of the spar. The hinge is of steel, 8 mm thick except for the central block, which is 36 by 36 mm. The top of the spar is a single piece of spruce, 22 mm high, 75 mm wide, and 4 m long. The bottom is of two pieces, each 22 mm thick, 100 mm high, and 4 m long, glued face to face.

15

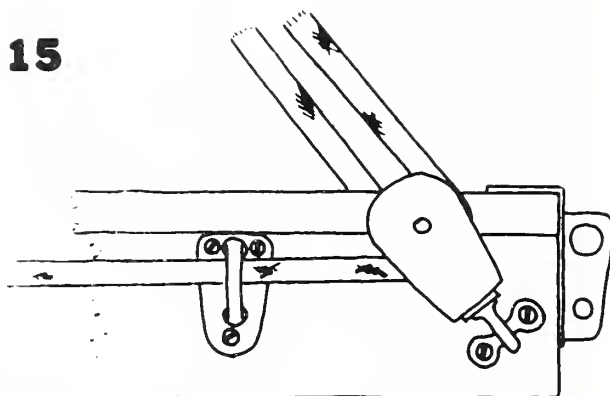


Figure 15. The outboard end of the spar. Note that the supporting ropes are not fastened to the outboard end. They pass through blocks and guides on opposite sides of the spar and are secured at the hinge end.

circumstances it should be possible to raise the spar from the ground and have it ready for use in 2 hours or less; in difficult circumstances it may take a full day.

Figures 14-17 illustrate the construction and operation of the spar.

The ropes used to support the outboard end of the spar are of nylon, but, unlike those used in climbing, are of a special braid which minimizes stretching (Samson Yachtbraid). This prevents the spar from sagging out of position as the weight of the climber moves away from the tree.

Note that the ropes supporting the spar are fastened at the inboard end of the spar, not at the outboard end. The position at which the spar rests depends upon the relative tension on these ropes. Thus a climber on the spar may maneuver herself through 180° of arc, without returning to the trunk, by pulling on

one or the other of the ropes running along the spar.

The climber sits in a "swing seat" suspended by loops of webbing. A climbing stirrup permits her to move along the spar by alternately sitting in the seat while she moves the stirrup and standing in the stirrup while she moves the seat.

In moving the spar, the ropes are coiled and the hinge is folded back along the spar and fastened. In placing it on the tree, it is hung, hinge downward, and maneuvered until the hinge is in place. The hinge is fastened to the tree with lag screws. Then the outboard end is lowered into place. In removing the spar the process is reversed.

The use of these three techniques in combination enables the climber to work with comparative freedom and safety for hours at a time if need be.

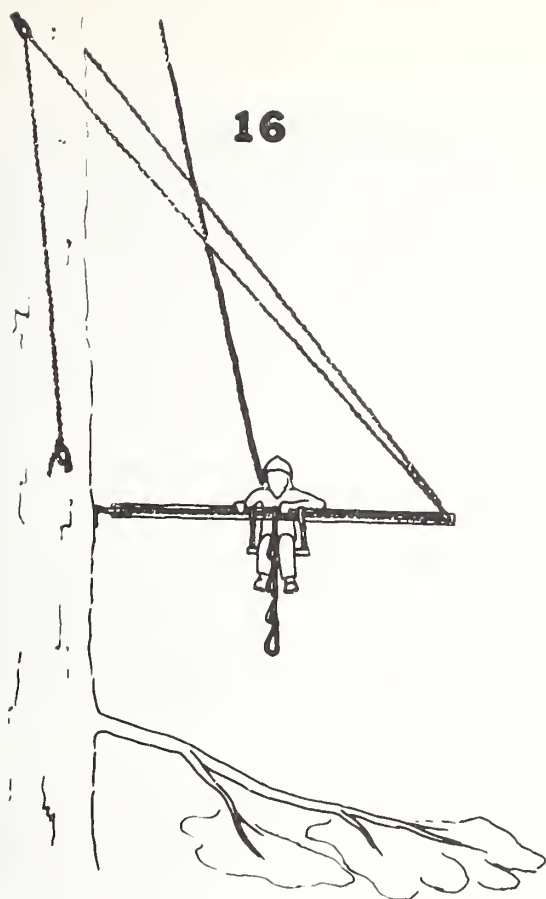


Figure 16. The spar in use. The suspending ropes pass upward through carabiners on opposite sides of the tree and are tied off near the inboard end of the spar. The spar is shown in the open but would normally be placed adjacent to a branch system.

Tree Description and Measurement

Description and measurement of a tree proceeds in two steps: an initial survey, in which the trunk and all of the branches are described, followed by detailed measurement of a sample set of branch systems. The tree is arbitrarily subdivided into components: the main trunk plus a number of branch systems. A branch system is defined as one or more branches, living or dead, arising from the same point on the trunk. Several branch systems may arise at the same height, but at different points around the circumference of the trunk. For examples of kinds of data recorded and calculated, the reader should refer to table 1

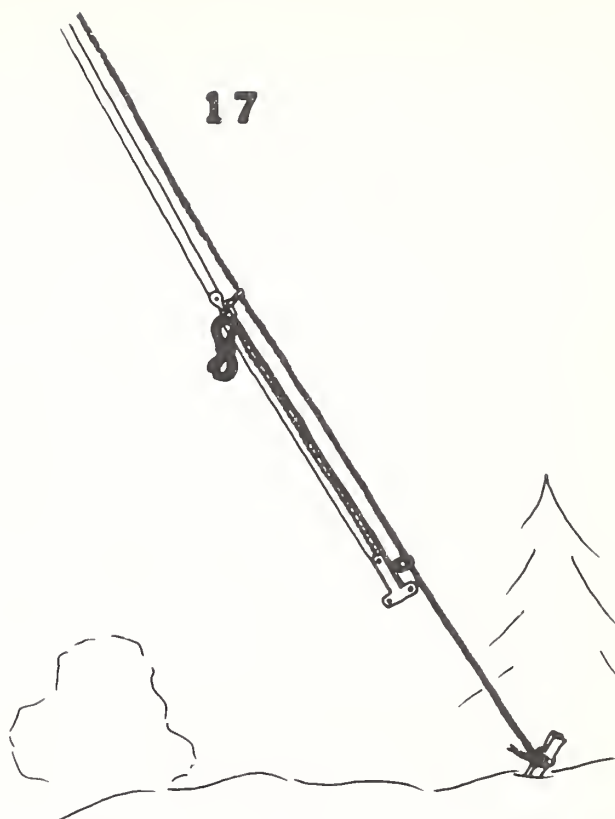


Figure 17. Raising the spar. A "trolley" of light nylon line is stretched from a clear area on the trunk to an open area on the ground. The spar is packaged, with its ropes coiled and hinge folded, and clipped to the "trolley" with carabiners. A handline and pulley aid the climber in pulling the spar up into the tree.

while reading the following sections.

Survey

As the tree is climbed, the trunk is marked off vertically in meters, by use of tape. At convenient intervals, 5 to 10 m, a benchmark is established and its height verified by transit from the ground. The diameter and inclination of the trunk are recorded at the benchmarks. It is not safe to climb above the point where the trunk is 10 cm or less in diameter, so we have treated the portion above that point as an exceptional branch system. When, through damage to the original leader, one or more secondary leaders have developed, they are treated in the same fashion as the main trunk.

Each branch system is numbered. The position of each branch system on the trunk is recorded by height and compass quadrant. Each branch system is scored for 10 variables. Most of these variables relate to the structure and biomass of the tree, but since this study began as a survey of epiphyte distribution, three variables relate to epiphyte load.

1. Number of Main Axes

A "main axis" is defined as a branch more than 4 cm in diameter, originating within 1 dm of the trunk. Six classes are recognized: no axes (i.e., no branch more than 4 cm in diameter), one axis, two axes, three axes, four axes, and five or more axes.

2. Extension from Trunk

The extension is measured as the horizontal distance from the trunk to the furthest tip of any part of the branch system. Five classes are recognized: 0-1 m, 1-3 m, 3-5 m, 5-10 m, and more than 10 m.

3. Total Length of Living Axes

An "axis" is any branch more than 4 cm in diameter. The total estimated here is of the length of all living axes within the branch system. Six classes are recognized: 0-1 m, 1-5 m, 5-10 m, 10-15 m, and more than 20 m.

4. Total Length of Dead Axes

The definition and classes are as in 3 above, except that here the branches are dead.

5. Area of Branchlets and Foliage

An estimate is made of the area of an imaginary figure formed by connecting the outer tips of all branchlets with the point of attachment to the trunk and projecting the outline on a horizontal plane. Six classes are recognized: 0-1 m², 1-2 m², 2-5 m², 5-10 m², 10-20 m², and more than 20 m².

6. Density of Branchlets and Foliage

Within the area delimited in 5 above, an estimate is made of the area occupied by branchlets and foliage. Six classes, expressed as percents of the total area, are recognized: 0 percent (no foliage), 0-20 percent, 20-40 percent, 40-60 percent, 60-80 percent, and 80-100 percent.

7. Maximum Diameter of Axis

The maximum diameter of the largest axis is measured to the nearest centimeter.

8. Lichen Cover: All Species

The lichen cover is estimated for all axes in

the branch system. Only foliose and fruticose species are counted. The cover is expressed as a percent of the total surface area on all axes. Six classes are recognized: 0 percent (no lichens), 0-20 percent, 20-40 percent, 40-60 percent, 60-80 percent, and 80-100 percent.

9. Lichen Cover: *Lobaria* species

The cover is estimated and expressed for *Lobaria* species alone, using the same classes listed in 8 above.

10. Bryophyte Cover: All Species

The cover is estimated and expressed for all bryophytes using the same classes listed in 8 above.

The data from this survey are tabulated, with the branch systems arranged by number, in the order in which they occur on the tree. A sample group of branch systems is then selected for detailed measurement.

Sample Selection

The number of branch systems selected for detailed measurement (n) depends upon the complexity of the tree: two branch systems are selected in a small, uniform tree; three, in a normal tree; four or five, in a tree with more than one leader. In our example, five branch systems were selected and measured.

An importance value (v) is calculated for each branch system according to the following formula:

$$v = b^2 + b_1^2 + ad + l + m$$

where,

b = class number (1-6) of total length of living axes

b_1 = class number (1-6) of total length of dead axes

a = class number (1-6) of area of branchlets and foliage

d = class number (1-6) of density of branchlets and foliage

l = class number (1-6) of lichen cover, all species

m = class number (1-6) of bryophyte cover

The importance value is listed for each branch system, and both running totals and a grand total (V) are calculated. The grand total (2,111 in our example) is set equal to the number of branch systems to be selected (five

in our example) and the running totals recalculated. For example, branch number 87 has an uncorrected running total of 28. The corrected total is: $28(5/2,111)=0.066$. After this correction, each branch system is represented by an interval, proportional to its importance value, which is the difference between its corrected running total and that of the preceding branch system.

A random number is drawn: a three-place fraction of 1.000. In our example, the number drawn was 0.870. Those branch systems are selected which have intervals which include: the random number, 1 + the random number, 2 + the random number, etc. In our example, the numbers 0.87, 1.870, 2.870, 3.870, and 4.870 corresponded to branch system numbers 7, 33, 61, 93, and 116.

The branch systems selected in this way are measured in detail as described below.

Branch System Measurement

The measurement of each selected branch system is carried out in 10 stages. The first four stages occur in the field and require the use of the spar; the remaining stages occur in the laboratory.

1. Each axis is marked off in decimeter lengths and the total length of the main axes is recorded.

2. The diameter is recorded every 4 dm.

3. The transition points (4-cm diam) at which an axis becomes a branchlet are identified.

4. At one-fourth of the transition points the distal portion, consisting of branchlets and attached foliage, is cut off and lowered to the ground for further study.

5. The annual rings are counted at the cut end of the removed branch and the age of the sample is recorded.

6. The foliage-bearing portion of each sample is cut into lengths bearing a single year's needles.

7. A subsample of 20 of each year's needles is measured (length and width) while fresh.

8. The foliage and attached fragments of branchlet are dried at 85° and weighed. The weight of each year's foliage is recorded, as is

the weight of its associated segments of branchlet.

9. The older branchlets, those without foliage, are cut into lengths representing approximately 1 year's growth and their lengths and diameters are recorded.

10. The segments of older branchlet are dried at 85° and weighed.

Analysis

Several types of information can be summarized from data accumulated by the techniques described. Two of these, surface area of the trunk and limbs and epiphyte biomass, are described in a paper by Pike et al.(1972). Analyses of wood and foliage biomass are being developed, but at present our results are incomplete since they are based on a single tree.

Another kind of analysis results in a diagram of the tree (fig. 18); a graphic summarization, to scale, of the structure of an individual tree. This diagram is an east-west vertical section. It serves both as a map for those working on the tree and as a chart of the distribution of branch systems and foliage.

Reconstruction of the trunk is based upon benchmark measurements of diameter, height, and inclination. A second leader, originating on the north side of the main trunk at the 40-m level, is drawn to the same scale but displaced to the right. Only those branch systems are shown which project to the east or to the west. From existing data one could draw a comparable north-south section displaying the remaining branch systems. Each branch system is shown in its correct position on the trunk and the length of the longest horizontal line indicates, to scale, the distance the entire branch system projected away from the trunk. However, the arrangement of axes and foliage within a branch system is symbolic rather than pictorial.

Living branch systems are represented by a parallelogram, representing foliage, usually accompanied by one or more solid lines, representing axes. Parallelograms without solid lines are branch systems in which no branch was more than 4 cm in diameter.

18

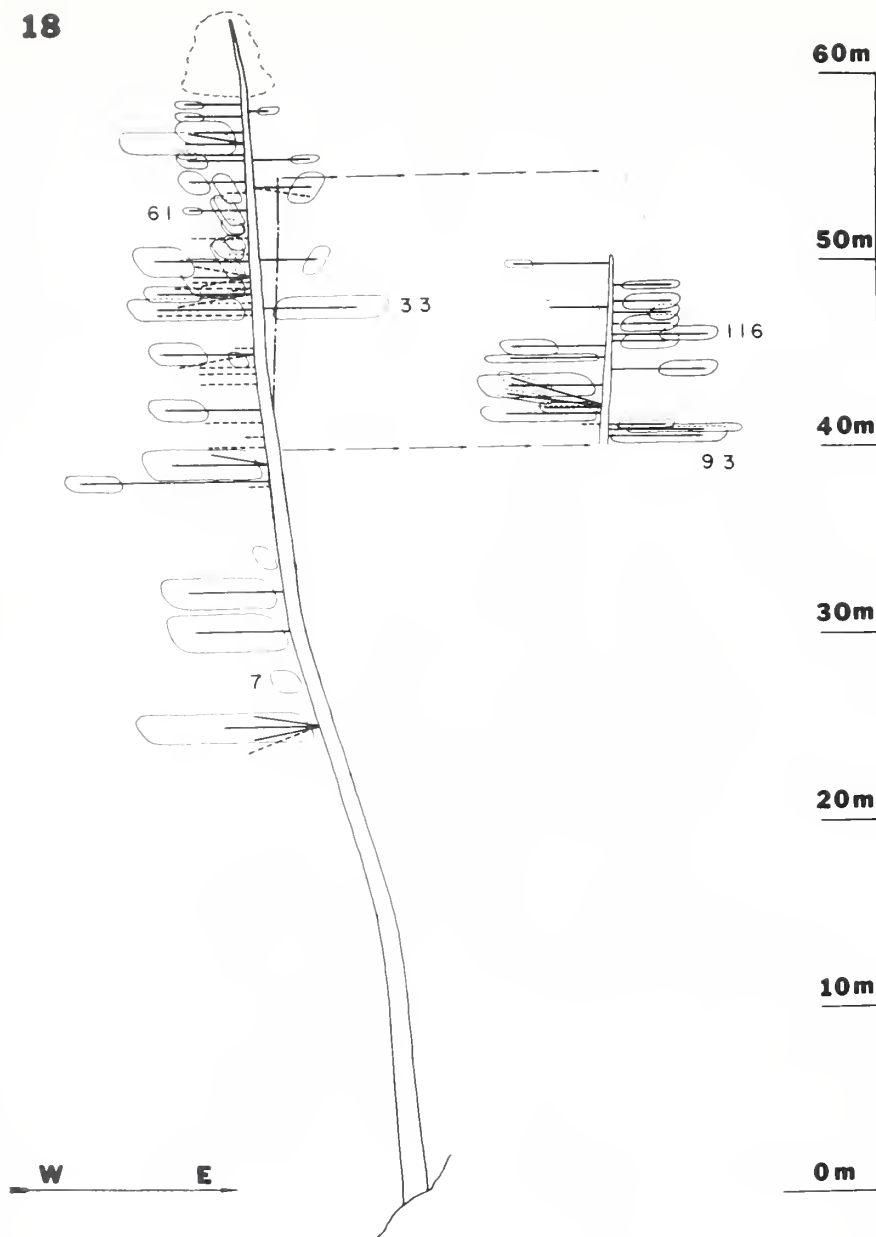


Figure 18. Semidiagrammatic reconstruction of Tree Number 1, Watershed 10. Only those branch systems extending to the east or west are shown. The second trunk is drawn to scale at the right height, but is displaced to the right. Solid horizontal lines represent living branches (axes) or branch systems more than 4 cm in diameter. The length of the line indicates, to scale, how far the whole branch system extends from the trunk. Dead branches are represented by dashed lines. The parallelograms represent branchlets and foliage. The length of a parallelogram represents the horizontal area covered by the branch system, and the height represents the density of branchlets and foliage within that area. Parallelograms without horizontal lines are branch systems with no branches more than 4 cm in diameter. Numbered branch systems are those selected for detailed measurement.

Dashed lines are dead branches. The area of a foliage parallelogram is a measure of the amount of foliage within the branch system. The length of a parallelogram is a function of the area of the branch system; the height of a parallelogram is a function of the density of foliage within the branch system.

Individual branch systems are easily identified. For example, those branch systems which were selected for detailed measurement (numbers 7, 33, 61, 93, and 116) are identified by number on the diagram.

Discussion

Although the access technique is still being improved, it is now very nearly routine for trees with a growth pattern similar to Douglas-fir. It could undoubtedly be modified for use in measuring large trees with different growth patterns. It would be particularly interesting to attempt to apply the method to trees of the upper canopy in lowland tropical wet forests.

We have not had adequate opportunity to evaluate the accuracy of our methods of description and measurement. The basic pattern seems satisfactory, but there will be changes made before we extend it to additional trees. We will increase the precision of initial estimates of lengths of axes. We need better methods for estimating foliage biomass. The importance value used in selecting branch systems combined values for foliage biomass with values for epiphyte load. This resulted in selection of a subset that was a poor compromise between the conflicting requirements for measurement of tree biomass and measurement of epiphyte biomass. In the future, separate importance values will be calculated for tree biomass and epiphyte biomass; and separate sets of branch systems will be selected and measured.

Acknowledgments

The authors are grateful to many people who contributed to the development of this project. Don Kirkpatrick taught us the ascent

technique and made the first ascent. Other climbers (Diane Nielsen, Tom Denison, Jane McCauley, and Karen Berliner), working with the authors, have helped in data taking and have made improvements in climbing methods. Dr. Jack Culver (Benton Boat Works) suggested improvements in the design of the spar, and James Ewanowski (Arboreal Constructions) built it. Sue Carpenter helped with the drawings. Dr. Scott Overton suggested the basic format of the sampling pattern and has guided its development.

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Table 1.—Exemplary data for branch systems on tree #1—a Douglas-fir on Watershed 10, H. J. Andrews Experimental Forest

Branch #	Height —m—	Compass Direction	Main Branches #	Extension from Trunk —m—	Total Length of Branches		Maximum Diameter —cm—	Area of Branch System —m ² —	Density of Foliage —%—	Lichen Cover		Bryophyte Cover —%—	Importance Value #	Running Totals #
					Live —m—	Dead —m—				All Species —%—	Lobaria —%—			
88	59.1	TOP	1	1-3	1-5		30	2-5	10-20	40-60	40-60		15	15
87	59.1	S	1	1-3	1-5		5	1-2	20-40	0-20	0-20		13	28
86	58.8	W	1	1-3	1-5		6	1-2	0-20	0-20	0-20		11	39
85	58.5	E	1	0-1	0-1		5	0-1		0-20	0-20		5	44
84	58.2	W	1	1-3	1-5		5	1-2	0-20	0-20	0-20		11	55
83	58.2	N	1	1-3	1-5		8	0-1		0-20	0-20	0-20	9	64
82	58.2	S	1	0-1	0-1		5	0-1		0-20	0-20	0-20	6	70
81	57.6	S	2	1-3	1-5		6	2-5	20-40	0-20	0-20	0-20	17	87
22	41.1	W	1	1-3		1-5	9	0-1		40-60	0-20	0-20	11	949
21	40.8	W	1	0-1		0-1	6	0-1		0-20			5	954
20	40.2	W	1	1-3		1-5	8	0-1				0-20	12	966
At this point the second trunk leaves the tree, 40m, N Compass														
19	39.3	W	2	3-5	5-10		7	5-10	60-80	0-20	0-20	0-20	33	999
18	38.4	W	1	5-10	5-10		8	2-5	20-40	20-40	0-20		22	1021
17	38.1	W	1	0-1		0-1	3	0-1		80-100			9	1030
2	20.4	N	5	3-5	10-15		8	10-20	40-60	0-20	0-20	20-40	41	1378
1	15.9	N	4	3-5	10-15	5-10	10	10-20	60-80	0-20		20-40	55	1433
Data for trunk 2 which left the tree between branch 19 & 20														
128	49.8	W	1	3-5	1-5		6	1-2	0-20	0-20	0-20	0-20	12	1445
127	49.5	N	1	3-5	1-5		6	1-2	0-20	0-20	0-20		11	1456
93	40.5	E	1	3-5	1-5		12	5-10	20-40	0-20	0-20	20-40	21	2062
92	40.5	N	1	1-3	1-5		9	0-1		20-40	0-20	20-40	11	2073
91	40.2	N	1	0-1	0-1		9	0-1		0-20	0-20	0-20	6	2079
90	40.2	N	1	3-5	5-10		11	2-5	20-40	0-20	0-20	20-40	23	2102
89	39.9	N	1	1-3	1-5		7	0-1		0-20	0-20	0-20	9	2111

Estimation of biomass and transpiration in coniferous forests using tritiated water

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Abstract

Nondestructive measurement of biomass and transpiration rates in trees is dependent on a new application of the established theory of tracer dynamics in steady state systems. The method utilizes HTO as a tracer for H₂O in the plant. Both transpiration and biomass measurements require experimental determination of tritium activity in the tree as a function of time. Biomass measurement requires one additional parameter—the mean residence time of water in the plant. In this paper we examine various theoretical and experimental alternatives for determining mean residence times. Data supporting one alternative is presented. The measurement of conducting tissue biomass is also discussed.

Introduction

Kinetic theory and tracer distribution methods have been used extensively in measurement of the properties of flowing systems both in biology and engineering. The theoretical aspects and the underlying assumptions governing the practical application of tracer dynamics have been thoroughly discussed by authors in many fields. Reports by Zierler (1964), Bergner (1961, 1964a, 1964b, 1965, 1966), and Ljunggren (1967) have described the use of tracer dynamics and kinetic theory in the nondestructive measurement of flow rates, mean residence times, and compartmental volumes of steady state biological and engineering systems.

It is the purpose of this paper to present the state of the art in the application of the theory and tracer methods to the nondestructive measurement of tree biomass and transpiration, and to examine the experimental parameters that can be measured as well as the underlying theoretical assumptions on

which they are based.

The nondestructive measurement of transpiration rates and biomass in trees utilizes tritiated water (HTO) as a tracer for water. Tritiated water is added to the tree water pool by injection into the trunk near ground level. The fate of the HTO tracer-labeled water in a tree is followed by monitoring tritium activity, as a function of time, in foliage and small branches. Both transpiration and biomass measurements require experimental determination of tritium concentration-time curves. Biomass requires additionally the mean residence time of water in the tree and the mean moisture content of the tree.

Theoretical Discussion

Transpiration Measurement

Application of the theory of tracer dynamics to the problem of measuring transpira-

tion rates in plants has been previously demonstrated^{1 2} (Kline et al. 1970). The theory itself has been discussed extensively by Bergner (1961, 1964a, 1964b, 1965, 1966), Zierler (1964), Ljunggren (1967), and Orr and Gillespie (1964). Transpiration measurements depend upon use of the Stewart-Hamilton equation shown by equation 1:

$$M = F \int_0^{\infty} f(t) dt \quad (1)$$

where M = total activity of tritium initially injected (disintegrations per minute, DPM),

F = the flow rate of water through the tree (ml/hour x tree),

$f(t)$ = activity distribution of tritium at the points of exit from the system (DPM/ml), and

t = time (hr).

Equation 1 states simply that the product of the flow rate (F) and the total integral of the curve of activity versus time (fig. 1) is equal to the total activity of the tracer which was originally injected. In practice the activity-time curve is measured experimentally and the total activity injected is fixed by the experimenter. The flow rate (F) is the only unknown quantity in equation 1 and is solved algebraically. The value of F is the daily flow rate which is averaged over daytime and nighttime flows. The average is taken over the full time interval of residence of tritium in the tree. Shorter term resolution of transpiration is not possible with this method. Examples of transpiration rates which have been obtained using equation 1 with tritiated water as the tracer are given in table 1 for field-grown coniferous trees.

¹ J. R. Kline, C. F. Jordan, and R. C. Rose. Transpiration measurements in pines using tritiated water as a tracer. In D. J. Nelson (ed.), Third National Symposium on Radioecology, Proc., May 10-12, 1971, Oak Ridge, Tenn. (In press.)

² J. R. Kline, M. L. Stewart, C. F. Jordan, and Patricia Kovac. Use of tritiated water for determination of plant transpiration and biomass under field conditions. In Symposium on the Use of Isotopes and Radiation in Soil-Plant Research Including Applications in Forestry, Proc. Int. At. Energy Agency Conf. SM-151, December 13-17, 1971, Vienna, Austria. (In press.)

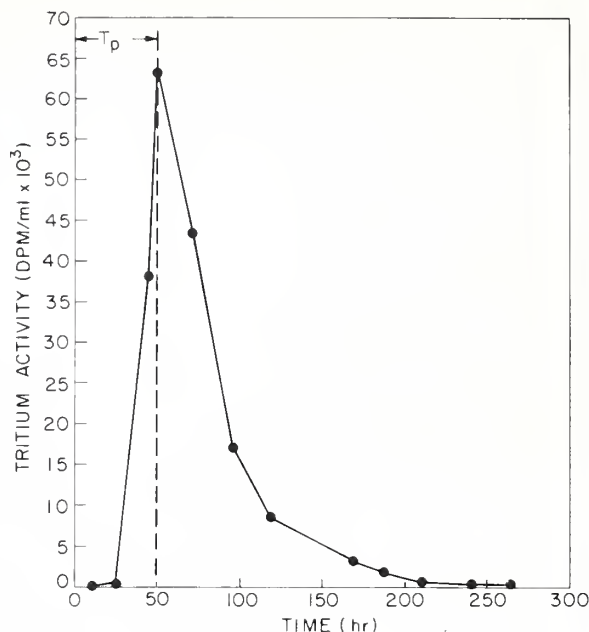


Figure 1. Typical activity-time response curve obtained by injecting a jack pine (*Pinus banksiana*) tree with tritiated water and sampling twigs as a function of time for tritium content. Peak arrival time is indicated by T_p .

Biomass Measurement

The measurement of tree biomass is based on that part of the theory of tracer dynamics which permits calculation of the pool size of the compartment through which flow takes place. In trees the pool refers simply to the average total water content of the tree. When pool size has been computed, it is a simple matter to convert to biomass using the average moisture percentage of the wood.

Derivation of an expression which permits computation of compartmental pool size is given by Zierler (1964). Zierler's expression is given by equation 2:

$$C = F \cdot T_m \quad (2)$$

where C = compartment volume (ml),

F = flow rate through the compartment (ml/hr), and

T_m = mean residence time of the flowing substance (hr).

Equation 2 states simply that the compartment pool size is given by the product of the

Table 1.—Transpiration rates, mean residence times, computed biomasses, and observed biomasses for field-grown red and jack pine trees

Red pine (*Pinus resinosa*) (1970)

Tree number	Dbh (CM)	Transpiration rate (F) (ml/hr)	Mean residence time (T _p) (hr)	Computed dry biomass (kg)	Observed dry biomass (kg)
3	14.1	1170	50	42.4	42.6
4	9.5	222	110	17.7	12.2
5	12.1	935	42	28.4	26.3
6	13.3	1280	42	38.9	35.1
7	12.3	725	49	25.7	26.7
8	8.2	413	49	14.6	12.1
10	12.3	254	98	18.0	20.6
Mean tree weight ± SE				26.5 ± 4.1	25.1 ± 4.3
Mean forest biomass ± SE (kg/ha)				7.7 × 10 ⁴ ± 1.2	7.3 × 10 ⁴ ± 1.2

Jack pine (*Pinus banksiana*) (1971)

Tree number	Dbh (CM)	Transpiration rate (F) (ml/hr)	Mean residence time (T _p) (hr)	Computed dry biomass (kg)	Observed dry biomass (kg)
1	10.5	807	49	38.5	19.9
2	12.0	833	52	33.5	26.7
3	10.0	540	48	21.5	19.9
4	10.0	941	27	25.6	32.0
5	8.9	570	45	25.4	18.1
6	11.0	833	25	19.2	26.0
7	11.0	609	23	17.0	32.3
8	9.5	506	46	24.6	24.6
9	10.4	492	27	18.3	20.9
11	11.4	1083	26	28.0	28.5
12	9.4	903	24	27.2	20.0
Mean tree weight ± SE				23.3 ± 2.0	24.4 ± 1.5
Mean forest biomass ± SE (kg/ha)				6.3 × 10 ⁴ ± 0.5	6.1 × 10 ⁴ ± 0.4

flow rate and the mean residence time of the system.

In plants the pool size (C) is also given by the difference between wet and dry weight ($W-D$) of the plant. Moisture fraction is conventionally calculated by equation 3:

$$\frac{W-D}{W} = f, \quad (3)$$

where W = wet weight of sample (gm),

D = dry weight of sample (gm), and

f = fractional moisture content.

Equation 3 holds equally well for the case where the determination is done on the entire plant or for a representative subsample of the plant. In the case where the entire plant is the sample, $W-D$ can be substituted for C in equation 1 resulting in equation 4, which is an expression for the moist weight of the plant:

$$W = \frac{1}{f} F \cdot T_m. \quad (4)$$

Moist weight can be converted to dry weight using equation 3. This results in equation 5 which is an expression for dry biomass of the plant:

$$D = \frac{1-f}{f} F \cdot T_m. \quad (5)$$

Equation 5 requires the experimental determination of f , F , and T_m for its solution. In the absence of a feasible method for determining f on the entire tree, it is necessary to measure it on subsamples. Ideally the subsamples should be weighted for different tree parts such as trunk, branches, and leaves. Since there is usually no method available for measuring weighting factors, we have followed the practice of estimating moisture content of the tree trunk since this represents the greater portion of the biomass of the tree. In our experience, moisture content of plant parts has not been greatly different from one another and no serious errors are introduced by following this procedure. If plants are found where unweighted estimates of f differ from the true weighted value, then this could be a significant source of error in the estimate of biomass.

The value of F in equation 5 is the mean flow rate which has previously been calculated using equation 1. This means that the reliability of the estimate of biomass can be no better in general than the reliability of flow or transpiration rate. Biomass estimates are normally expected to have lower statistical precision than transpiration estimates since they require the use of additional measured parameters.

The most difficult parameter to measure in equation 5 is T_m , the mean residence time. There appear to be at least three possible approaches to obtain this quantity: (1) measure the slope of the declining branch of the activity-time curve; (2) compute the first moment of the curve; or (3) measure the transit time between the point of injection and the point of exit of the tracer from the system (Donato et al. 1964).

The slope method for mean residence time would be valid in the case where the plant is labeled to equilibrium with the tracer. If all of the water molecules of the trees were labeled equally with HTO, then the rate at which tritium activity declines in the tree would be proportional to the amount of tritium present. Such systems are described by an equation of the form $A = A_0 e^{-\lambda t}$ where A_0 is initial activity, A is activity at time t and λ is the rate constant of loss. The term λ is the slope when data described by this relationship are plotted on semilogarithmic coordinates. The mean residence time for such a relationship is simply the reciprocal of λ ($T_m = \frac{1}{\lambda}$).

This is a frequently used relationship for obtaining T_m although in practice it is sometimes used without verification of the assumptions. In some systems it is possible to label to equilibrium by injecting the tracer into the system continuously; however, in large trees this would entail larger than desirable releases of radioactivity to the environment. Therefore, it is preferable to label by the instantaneous pulse method. When the pulse method of labeling is used, the injected material moves upward in the tree while retaining its pulse shape. The pulse may undergo considerable broadening but the system cannot be assumed to have achieved uniform labeling. In

this case the slopes of activity-time curves have two components, one reflecting the turn-over rate of water and the other reflecting the pulse shape. There is no method currently available for resolving these components in an activity-time curve, and therefore the slope of the curve cannot validly be used to compute T_m .

Ljunggren (1967) has described the computation of mean residence times for flowing systems using the first moment of the activity-time curve. The first moment is the centroidal axis of the activity-time distribution—that vertical axis which divides the distribution into two parts having equal areas. Equation 6 indicates the method:

$$T_m^* = \frac{\int_0^\infty t f(t) dt}{\int_0^\infty f(t) dt} \quad (6)$$

In general, T_m^* will always be the true mean residence time of the tracer in the system under study. The tracer mean residence time of the system will satisfy the relationship of equation 2, however, only under the conditions of identical behavior of tracer and substance traced. In trees, the nominal mean residence time for water, T_m , is not equal to the tracer mean residence time T_m^* since the tracer apparently undergoes interactions with the conducting vessels of the tree. The relationship is given by the expression

$$T_m^* = f_1 T_m + f_2 T_H$$

where T_H is the residence time of the fraction of tritium which has undergone some interaction with the wood and f_1 and f_2 are fractions of the total tritium which pass through the tree without interaction and with interaction, respectively. Possible interactions include isotopic exchange of tritium with hydrogen of the wood or diffusion of tritium into nonflowing compartments of plant water. Experimentally $T_m^* > T_m$ has been found for all trees which have been examined to date, indicating that the term $f_2 T_H$ has a nonzero value in trees. This phenomenon has been termed "holdback" by others who have

examined tracer dynamics in flowing vessels (Ljunggren 1967). Because of "holdback" the value of T_m^* cannot be used without correction to solve equation 2. The problem of finding an appropriate value for $f_2 T_H$ is presently unsolved.

In general, the mean residence time for a flowing system can always be obtained by measuring the activity distribution of a tracer in the system at two points along the flow pathway (Ljunggren 1967). If T_1 is the time of passage of the tracer at point 1 and T_2 the time of passage at point 2 further downstream, then $T_m = T_2 - T_1$ where T_m is the mean residence time between the two sampling points. Since the tracer normally undergoes peak broadening, T_1 and T_2 are taken as the times when the peak of the distribution passes the sampling points. In trees we fix the initial position of the tracer by the injection at time $T_1 = 0$. In this special case $T_m = T_2$. The value of T_2 could be measured at any point in the tree downstream to the injection point. In the special case where the downstream sampling point is tree foliage, then $T_m = T_p$ where T_p is simply the time of peak arrival in the foliage.

As a first approximation it can be assumed that T_p is not affected by "holdback" as was T_m^* because tritium is probably removed from free flowing forms equally over the entire activity distribution. That is, interaction of tritium with conducting vessels could as well occur with the isotope in the leading edge of the distribution or the trailing edge. The peak position would, therefore, not be affected by these interactions. This assumption requires experimental verification which is given in the results section.

Correction for Nonconducting Tissue

The foregoing suggests that tritium tracer experiments can only be used to measure actually conducting biomass in trees. Such tissues as bark, flowers, fruit, and nonconducting heartwood will not be included in the estimate. Roots are not included in the estimate since the tracer injection is normally done in tree trunks above the roots. In practical biomass measurements for forestry purposes, the

most serious problem is the omission of non-conducting heartwood from the direct measurement. The theory of tracer dynamics cannot be used for direct measurement of this quantity, and it is, therefore, necessary to make an approximation. Equation 7 expresses the relationship between total biomass and the biomass of heartwood and sapwood:

$$V_T \rho_T = V_H \rho_H + V_S \rho_S, \quad (7)$$

where V_T = total volume of tree tissue (cm^3),

ρ_T = weighted mean wood density ($\frac{\text{g}}{\text{cm}^3}$),

$V_H; V_S$ = volume of heartwood and sapwood (cm^3), and

$\rho_H; \rho_S$ = density of heartwood and sapwood ($\frac{\text{gm}}{\text{cm}^3}$).

Substituting the relationships

$$\rho_H / \rho_S = K \quad \text{and} \quad V_H / V_S = \lambda$$

into equation 7 results in equation 8:

$$V_T \rho_T = V_S \rho_S (\lambda K + 1). \quad (8)$$

Assuming that the volume of heartwood and that of the total tree can be approximated by a right circular cone, an expression for λ is derived as follows:

$$\lambda = \frac{r^2}{\Delta r (2r + \Delta r)},$$

where r = mean radius of heartwood at base (cm), and

Δr = mean thickness of sapwood at base (cm).

Upon substituting for λ in equation 8, a final expression for tree biomass is obtained:

$$V_T \rho_T = D = V_S \rho_S \left(\frac{r^2 K}{\Delta r (2r + \Delta r)} + 1 \right). \quad (9)$$

The numerical group $V_T \rho_T$ is the total plant biomass (D) and the group $V_S \rho_S$ is the conducting or sapwood biomass as measured by the tritium method. Equation 9 is not sensi-

tive to the assumption that wood volumes are approximated by right circular cones. The same result is obtained for a right circular cylinder or for intermediate figures.

Equation 9 has not yet been evaluated experimentally. It is proposed here to suggest some of the anticipated lines of research to be undertaken in the Coniferous Biome. A principal problem for the solution of equation 9 lies in accurate measurement of the quantities r and Δr . These quantities fundamentally refer to the radii of nonconducting and conducting wood, respectively. In the simplest case they may be coincident with heartwood and sapwood as observed visually. Their evaluation could then be done by straightforward measurement of tree cores.

An accurate solution also depends on the nature of the transition zone between conducting and nonconducting tissue. If this is sharply defined, then r and Δr will be well defined and an accurate solution to equation 9 can be obtained. If the conduction undergoes a gradual transition across the radius of the tree, there may be no practical method for assigning values to r and Δr . It is possible that reasonable values can be obtained by studying tritium distribution along wood cores which have been taken from tritium-labeled trees. These considerations apply to large trees which have appreciable volumes of heartwood. In the trees for which we have experimental data, heartwood was a minor part of the total tree volume and was not considered.

Results

The mean residence time T_m is the most difficult parameter of equation 5 to obtain, principally because it is not generally known a priori which of several possible means of computing it is the correct one. The desired value is the nominal mean residence time T_m (equation 2); however, in the usual non-destructive experiment this is not directly obtainable. Where tritium-injected trees have been harvested, however, the water pool size (C) is directly obtainable from biomass and moisture measurements, and it is possible to

solve equation 2 for T_m since the flow rate (F) is known. The values of T_m obtained by this direct method were compared to the values obtained by the three indirect methods which were previously discussed.

The nominal mean residence time (T_m) has been computed for several harvested field-grown coniferous trees and the values compared with those obtained from curve slopes, from first moment calculations and from peak arrival times. The results show in general that $T_m > T_S$ for slope calculations and $T_m < T_m^*$ for first moment calculations.

The nominal mean residence time agrees most closely with T_p which was obtained by the midpeak or peak arrival time method.

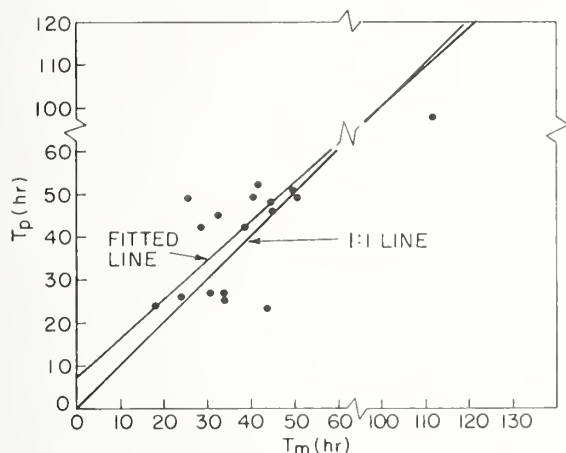


Figure 2. Relationship between nominal mean residence time (T_m) of plant water and mean residence time obtained by peak arrival (T_p) from activity-time curves.

Figure 2 shows the relationship between T_m and T_p for a group of harvested trees. The slope of the linear least squares relationship between the two estimates is 0.916, and the intercept is 7.05 as compared with the expected slope of one and expected intercept of zero (1:1 line, fig. 2). The coefficient of determination (r^2) is 0.70 for the relationship. The results suggest that T_p is an unbiased estimator of T_m . This confirms that T_p is the best estimate available for T_m since other known possibilities have been examined and found to be biased either above or below the true values.

The scatter of data points on figure 2 indicates that forest biomass determinations must

at present be approached statistically. Any particular determination of mean residence time of water may be substantially in error; however, a group of determinations appears to converge on the true T_m values of the group. Experimental error reduction is one objective of continuing studies in the Coniferous Biome program.

Table 1 shows a comparison between tree biomass as computed by equation 2 and actual harvested weights. These data were obtained in a uniform age plantation of red pine (*Pinus resinosa*) in 1970, and a similar stand of jack pine (*Pinus banksiana*) in 1971. The results show individual examples of substantial error; however, the estimates of mean tree biomass and mean forest biomass as measured by the tritium method agree well with those estimated by direct harvest. There is, of course, no necessity for determining biomass of a group of trees on all individuals simultaneously. Biomass can be determined at any time during which transpiration flow is taking place. The results suggest that the biomass of these forests could have been reliably determined by the tritium method alone.

Conclusions

Experiments designed to measure transpiration rates in field-grown trees may also be used with little extra data collection for non-destructively measuring tree biomass. The tritium method can, in general, be used only for determination of biomass which is actually transmitting water. Flowers, fruits, bark, and nonconducting heartwood are not included in the estimate. We have proposed a method for including heartwood in the estimate but have not yet proved it experimentally.

The most difficult parameter to obtain for calculation of biomass is the nominal mean residence time of water in the plant. After examining several alternatives for obtaining this quantity, we conclude from theory and experiment that the time of arrival of peak tritium activity in tree foliage is the most reliable estimate of nominal mean residence time. Estimates of biomass of field-grown coniferous trees show considerable statistical varia-

tion; however, the mean of a group of such determinations was a reliable and unbiased estimate of the mean obtained by direct harvest. With additional research on the problem it may be possible to reduce the experimental error of the method and to improve the reliability of individual estimates.

Acknowledgments

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Theodolite surveying for nondestructive biomass sampling

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Abstract

*By theodolite surveying, the relative location of points in space may be calculated by triangulation. With the aid of computers, data gathered by theodolite surveying may provide a dimensional analysis of individual trees. Because the system is nondestructive, the rates and patterns of change in the spatial structure of trees and stands may be monitored by repetitive surveying. This paper presents a preliminary test of the approach upon trees in a 40-year-old Douglas-fir (*Pseudotsuga menziesii*) plantation in western Washington. From experience gained in the initial experiment, recommendations are made to increase the precision of repetitive measurements.*

Introduction

The theodolite is an instrument used in precise surveying to locate points in space by triangulation. The use of high speed computers for converting angle measurements to point locations allows theodolite surveying techniques to be used for describing the physical structure of vegetation assemblages in considerable detail with relative ease. Such a surveying procedure has been used to construct simulation models for studying the effects of vegetation on engineering activities (West et al. 1971). Since the method is nondestructive, it offers the possibility of repetitive sampling with high inherent precision. Exploratory surveys were made recently to test the applicability of the system for this purpose (West and Allen 1971). This paper examines some data from a Douglas-fir stand at the Coniferous Biome intensive site in Washington.

Description of the Surveying System

The procedure requires two theodolites placed at an arbitrary distance apart and lo-

cated conveniently to the subject trees (fig. 1). The vertical and horizontal angles from each instrument to every point located in the sample space are measured with respect to a base line. The instruments can be moved about to obtain clear lines-of-sight to desired points in the sample space and every instrument location (turning point) is referenced to the base line by conventional traverse survey-



Figure 1. Instrument set-up for surveying spatial structures of trees. Two theodolites are in use; the instrument in the middle is a spotting laser.

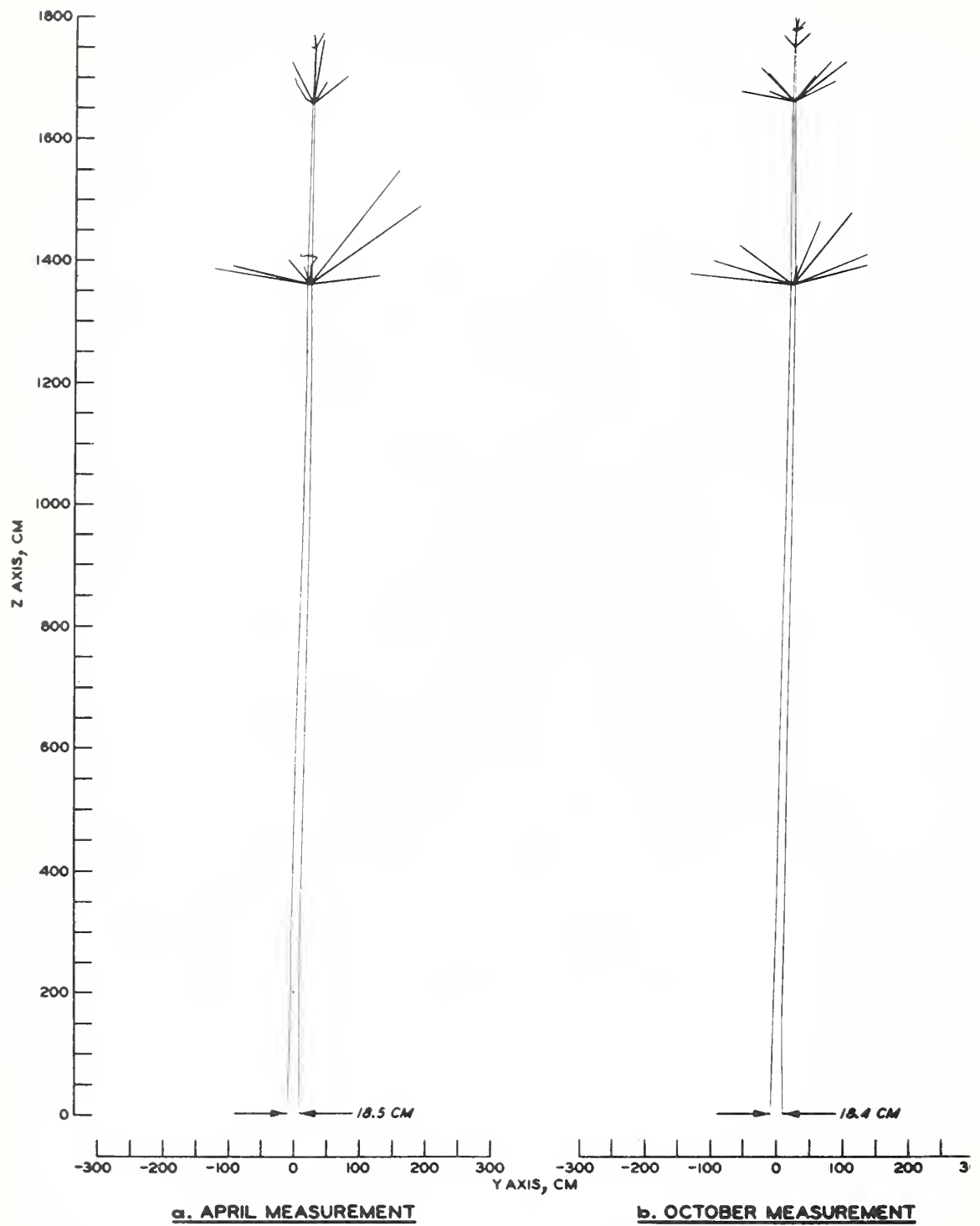


Figure 2. Graphic display of point location data from a Douglas-fir tree near Seattle, Washington, on which branching was not surveyed in detail. Bole graphed to show diameter to scale.

ing methods. Every point in the sample space is thus located with respect to any arbitrarily defined three-coordinate system. Details of the procedure are presented elsewhere (West and Allen 1971).¹

One of the theodolites is equipped with a specially designed circular reticle for measuring branch or stem diameter, employing the principle of stadia measurement. All measured angles and reticle readings are recorded in the field on specially designed data forms, and trigonometric conversions of field data to point locations and stem or branch diameters are made by computer. Figure 2 is an example of a computer graphic of one of the trees on the Thompson site.

Description of the Sample

The Douglas-fir stand, located on the A. E. Thompson Research Area in the Cedar River watershed, lies some 64 km southeast of Seattle, Washington. The Research Area is described in detail by Cole and Gessel (1968). Measurements were obtained from a group of eight contiguous trees on each of two proximate (not contiguous) permanent research plots (designated 1 and 2 on the Research Area) within an even-aged 40-year-old plantation. Plot 1 received three applications of nitrogen as ammonium sulfate $(\text{NH}_4)_2\text{SO}_4$ at the rate of 222 kg/ha in October 1963, October 1964, and May 1970. Plot 2 was left untreated as a control.

The eight trees selected for measurement on each plot were selected first by choosing an arbitrary point within each plot, and then taking the eight trees nearest to each point as sampling trees. The only controlling criterion placed upon location of the starting point on each plot was that it should be far enough within the plot to avoid inclusion of boundary trees in the sample. Measurements on the sample trees were made in April 1970, before bud burst, and then again in October 1970, after the apparent end of the growing season.

Data were taken to include the coordinate location and the diameter (outside bark) at the following points:

- a) At the base of the tree, defined as being at the duff line or ground line, as well as as could be determined. Diameters were measured with a tape.
- b) Diameters at breast height (d.b.h.) 150 cm above the duff line were marked with a ribbon for subsequent remeasurement.
- c) The bole at every fourth whorl where limbs were still present (diameters were calculated from reticle readings).
- d) The base of the live crown, defined as the lowermost whorl at which more than 50 percent of the branches held green leaves. The location of a whorl is defined as the approximate centroid of branch emergence; diameter measurements on the bole are made just below the lowermost branch as well as just above the uppermost branch of the whorl (fig. 3). (Diameters calculated from reticle readings.)
- e) At every fourth branch whorl within the live crown, or at least one branch whorl within the middle one-third of the live crown.
- f) The topmost whorl in April and that same whorl plus the new topmost whorl in October.
- g) The top of the leader, at the base of the terminal bud whorl.



Figure 3. Definition of branch whorl location, and location of diameter measurements at whorl.

¹E. E. Addor and H. W. West. A technique for measuring the three-dimensional geometry of standing trees. U.S. Army Waterways Experiment Station, Vicksburg, Mississippi. Unpublished.

- h) Point locations and diameters were measured for various defined points on crown branches but will not be discussed here.

A total of 30 turning points (instrument set-ups) were established for the April survey and all were referenced to a common coordinate system. The same points of reference were used again in October, but no deliberate attempt was made to duplicate the surveying sequence, e.g., to site each point on the tree and to measure each diameter from the same turning point. Nonetheless, the sequence that was adopted for the first survey was approximated during the second survey, as a result of constraints within the stand. Thus the sampled points were mostly viewed from the sample angles during both surveys. Since both surveys were referenced to the same coordinate system, the reported coordinate locations of surveyed points are in theory exactly comparable, so that any difference in the reported location of a point represents a displacement of that point by wind action, growth, or survey error.

Results of Theodolite Survey

Crown Cover and Stand Density

The crown cover was essentially closed and the branching structure relatively dense. The ground area occupied by the eight sampled trees on each plot was determined in April by traversing the ground points representing the outer crown limits of the outermost trees of the group. The crown coverage so determined was 31.2 m² on plot 2 (unfertilized) and 44.0 m² on plot 1 (fertilized) representing a crown area per tree of 3.9 m² and 5.5 m², respectively, or a density of approximately 2,567 and 1,818 trees per hectare.

In this same stand, in October, 1965, Dice (1970) destructively analyzed 10 trees from a 0.0045-hectare (45 m²) plot, which is 4.5 m² per tree, or approximately 2,222 trees per hectare. These values lie reasonably between

our values for the unfertilized and fertilized trees. Unfortunately we are not certain how the crown boundaries of his trees relate to the boundaries of his 45 m² plot.

The problem of the true relation of the crown cover per tree (tree mean area) to sample plot boundaries is controversial (Greig-Smith 1964). Supposedly, tree randomness with respect to sample-plot boundaries should balance the excluded and included portions of included and excluded trees, but the true relation is apparently complicated by both plot size and plot shape. A crown-limit traverse is relatively simple with a theodolite survey and is easily converted to area by the computer. It should therefore be worthwhile to examine whether such a procedure would resolve the problem of the relation between sample plot boundary and tree crown boundary in the determination of crown cover, stand density, or tree mean area.

Patterns in Diameter Measurements

Examination of the diameter data from the theodolite survey suggests that the unfertilized trees exhibited greater increment on the upper portion of the bole than on the lower, whereas the fertilized trees showed approximately equal growth pattern throughout the length of the bole. Such patterns seem reasonable because of the difference in stand density. Similar patterns have been reported in unthinned and thinned stands of Douglas-fir surveyed with an optical dendrometer over a 2-year period (Groman and Berg 1971).

Certain sources of inaccuracies in diameter measurements with the theodolite system should be mentioned. First, diameters calculated from reticle readings are dependent upon accurate measurements of the distance. Second, interpolation errors from this source may be important when estimating small branch diameters with the reticle. Countering these disadvantages is the possibility of measuring diameter at any point on a stem or branch regardless of the direction or angle of inclination. Other instruments such as the optical dendrometer have no reticle inscribed and thus are restricted to measuring bole diameter.

Patterns in Point Displacement

Measuring changes in the physical structure of vegetation consists primarily of simply measuring the displacement of defined points over a specified time interval. Obviously, an error in determining the location of a point either at the beginning or at the end of the time interval will result in an error in the measurement of displacement.

Measurement errors may stem from a variety of sources, depending upon the methods of measurement. Since theodolite surveying is dependent upon calculation of point locations by trigonometric relations, both instruments must be precisely sighted on the spot to be located. Disparities in the assumed location of the target point will cause errors in the calculated location of the point. Horizontal disparities will cause horizontal and vertical errors according to the angle of convergence and the slope of lines-of-site, while a vertical disparity will not locate a point at all.

To reduce errors from this cause, a spotting laser (fig. 1) can be used to project a bright orange spot a few millimeters in diameter onto the tree at the selected target point. This provides a definitive target for sighting the theodolites at one given time, but it does not resolve the problem of relocating the exact point of measurement for periodic remeasurement. The spotting laser was at the Thompson Site during both the April and October surveys, but it was inoperable much of the time. Periods of its use and nonuse may account for some of the patterns in the data.

Other sources of error include the usual reading and transcription errors by instrument men and note keepers. Errors from these various sources may or may not be critical, depending upon their magnitude and frequency, and the special purpose for which the survey is being made. For the purpose of monitoring subtle changes in the vegetation structure over a brief time period, even very small errors may be important. Gross anomalies in the data may be identified and approximately corrected during data editing and preliminary analysis, but small errors regardless of source may not be distinguish-

able from true displacement.

For the purpose of discussion, any difference between the calculated location of a defined point from one observation to another (specifically, for the present case, from April to October), in any coordinate direction, may be defined as an "apparent displacement" of that point in that direction. It can then be defined that the apparent displacement always consists of two components: True displacement resulting from changes in the shapes of the trees, and errors resulting from inaccuracies and mistakes in instrument reading, note keeping, and calculations. Hereinafter, these latter will be referred to collectively as "survey error." The question to be resolved, then, is what proportion of apparent displacement can be attributed to each of these two components. Data from the surveyed Douglas-fir stand provide an opportunity to examine the theodolite surveying system with respect to these problems.

Figure 4 is a set of graphs of the apparent displacement in the xy (horizontal) plane of defined points at various levels on the tree boles, as measured from April to October. They are: (A) at the base of the tree, (B) at the base of the live crown, (C) at an arbitrary intracrown whorl, and (D) at the whorl that was defined as the topmost whorl in April (i.e., at the base of the April leader, three trees are omitted from the intracrown whorl data due to omissions in the survey). With few exceptions, the apparent displacement in the horizontal plane at the base of the tree is within plus or minus 3 cm, with a slight systematic bias in the positive x direction and in the negative y direction, but with the points for the unfertilized and fertilized trees reasonably well interspersed. Since trees are anchored at the base, it may be assumed that any apparent displacement of the tree axis in the horizontal plane at that level must represent a surveying error. Therefore this slight systematic error at this level on these trees may be interpreted as a horizontal error in relocating the established origin of the coordinate system. The absence of a separation in this plane at this level between the apparent displacement of the unfertilized and fertilized

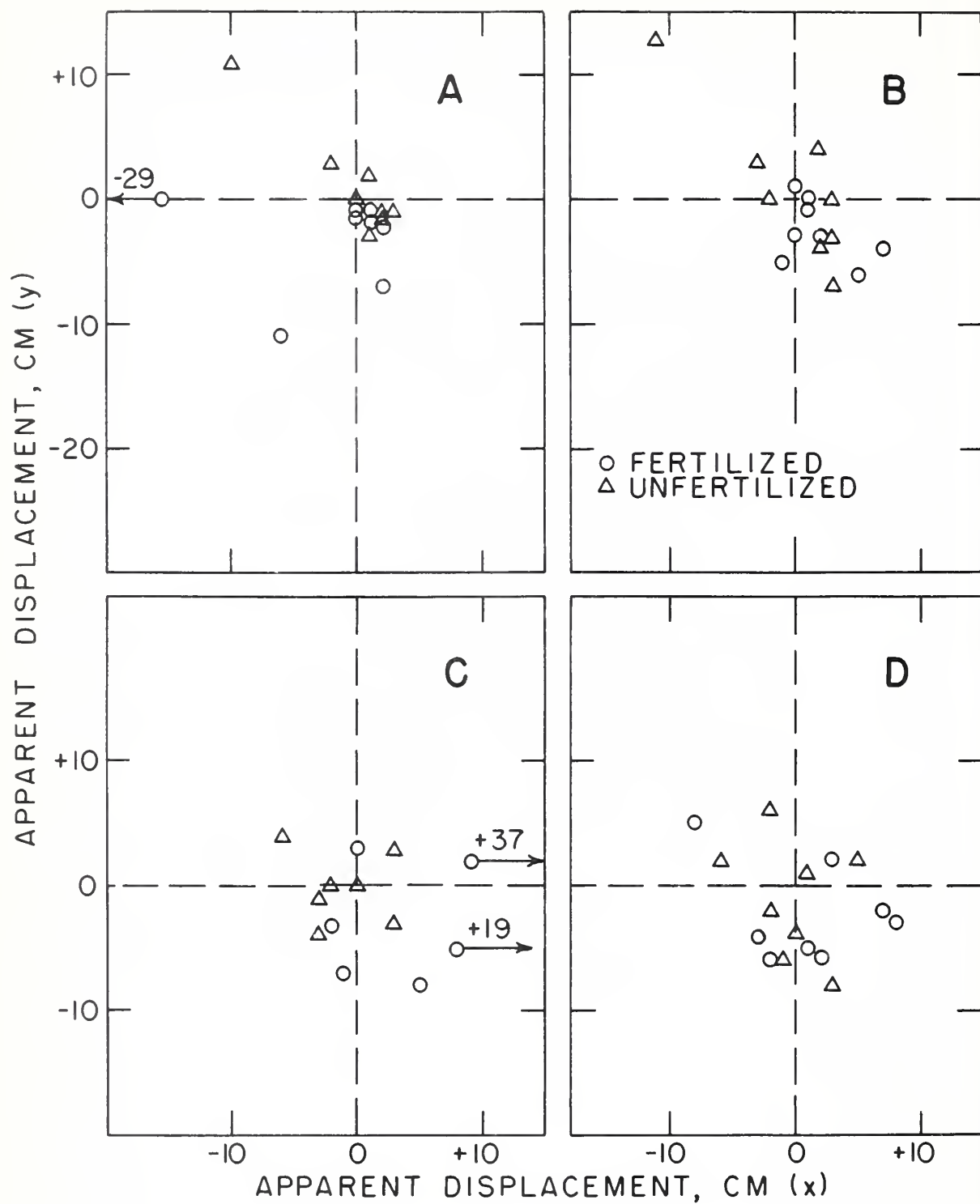


Figure 4. Apparent displacement of the tree boles in x and y (the horizontal plane) at various levels on the sampled trees, from April to October: (A) at the base of the trees, (B) at the base of the live crowns, (C) at an intracrown whorl, (D) at the base of the April leader (based on data from table 2 in West and Allen 1971).

trees indicates that the coordinate system was surveyed across the intervening distance between the two plots (about 20 m) with negligible error in this plane. If the data are adjusted for the horizontal error in relocation of the coordinate system origin, then the displacement error is quite small, and it must be conceded that remeasurement of the horizontal angles to the trees has been achieved with a fair degree of success, despite the 30 turning points used in accomplishing the survey.

Two explanations may be suggested for the increasing scatter of points in the horizontal plane with increasing height on the tree, shown on figure 4B, C, and D. First, it may be assumed that surveying errors have increased with increasing elevation of lines-of-sight, or second, it may be assumed that the position of the boles are less stable in the horizontal plane at higher levels on the tree. Since point locations in the horizontal plane are calculated from horizontal angles, irrespective of angles of elevation, there is no reason to assume that surveying errors should increase in relation to elevation. It follows therefore that errors in the location of points in the horizontal plane at any elevation might be equal to, but should not exceed, the errors in location of the base of the trees in this plane. It follows in turn that the apparent horizontal displacement of points on the upper boles of these trees must be a true displacement. The pattern is consistent with what would be expected as a result of movement of the trees by wind.

Figure 5 is a set of graphs of the apparent displacement of z (the vertical plane, or elevation) for the same defined points on the bole that are shown on figure 4, respectively. These show a considerable scatter in the apparent vertical displacement at the base of the live crown, moderate scatter in apparent vertical displacement at the intracrown whorl, and again a relatively close clustering of apparent displacement at the base of the April leader.

This pattern of variation may be attributed to relative differences in the difficulty of identifying the defined points with respect to elevation. This difficulty is more or less

inherent in the definition of the points; that is to say that "at or near the duff or ground line" is less definitive than is "the centroid of the branch whorl," whereas the topmost whorl (base of the leader) is the smallest and most definitive of the defined points. The differences in vertical scatter of points for the base of the live crowns and for the intracrown whorl may be attributed to errors of approximating the exact elevational location of the latter through obscuring branches and foliage. These inconsistencies of identification have important implications with regard to measurement of length relations, such as the total height of trees or the ratio of bole length to length of live crown (although, of course, the significance of the implication is determined by the magnitude of the dimensions and the special purpose for which the relations are being measured).

It was observed above that the apparent displacement of defined points on the unfertilized and the fertilized trees were reasonably well interspersed with respect to the horizontal plane. With respect to elevation, however, the data exhibit systematic tendencies that require explanation. Specifically, figure 5B shows a seemingly strong tendency toward a positive apparent displacement of about 6 or 7 cm for the base of live crowns on the fertilized trees, while the apparent displacement of this point on the unfertilized trees appears to be randomly dispersed about zero. A possible explanation is that a vertical error was committed in extending the coordinate system across the distance (approximately 20 m) between the two groups of trees. However, if this were the case, then the same apparent vertical displacement must occur at all other levels on the fertilized trees; if it does not, then its absence from other levels must be accounted for. The data for the intracrown whorl (fig. 5C), though somewhat more scattered than the data for the base of live crown, do indeed suggest a similar disparity between central tendencies for the two groups of trees, but a similar disparity is not obvious at the base of the trees (fig. 5A), nor at the base of the April leaders (fig. 5D). It may be that for the base of the tree, the disparity is simply obscured by the scatter of the

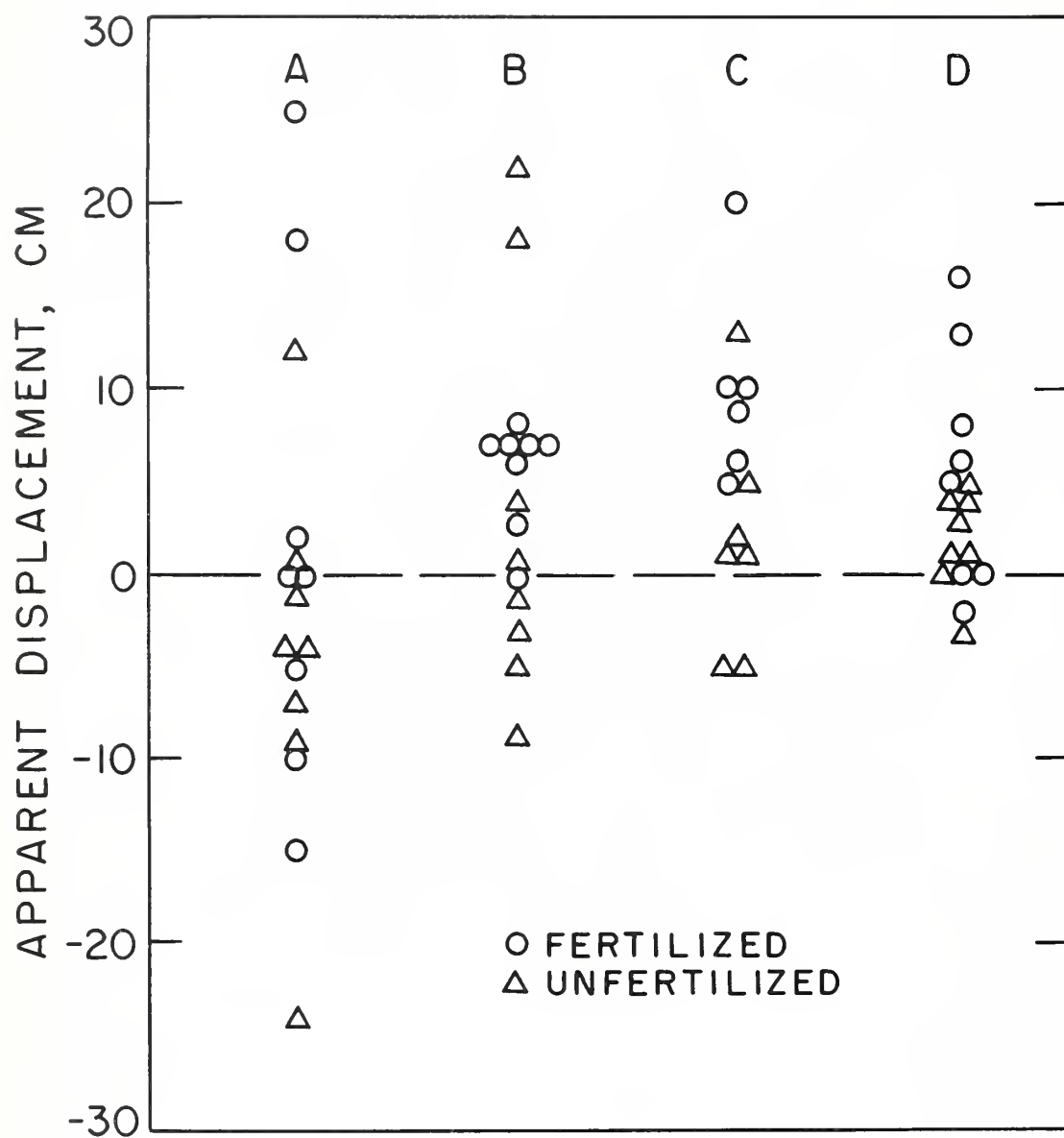


Figure 5. Apparent displacement of points on the tree boles in x and y as a function of z (elevation), from April to October: (A) at the base of the trees, (B) at the base of the live crowns, (C) at an intracrown whorl, (D) at the base of the April leader (based on data from table 2 in West and Allen 1971).

data; there is no obvious explanation for its absence at the base of the April leader.

Conclusions

The preliminary survey of Douglas-fir trees at the Thompson Site suggests that theodolite surveying is adaptable to the purpose of detecting and monitoring subtle patterns of change in vegetation structures. In terms of quantity and quality of data obtained for the energy expended, this procedure appears to be commensurate with any other known tree measurement system, and it offers advantages not offered by any other system. First, because the location of every point in the sample is determined relative to an arbitrary point defined as the origin of the coordinate system, the apparent displacement of any point on the tree is independent of the apparent location of any other point on the tree. Second, displacement of points in any direction can be measured with this procedure, such as, for example, the tips of branches radially disposed about the stem and growing at various angles from the vertical. Finally, and of considerable importance, this system is entirely nondestructive and is therefore well suited to continued monitoring of growth trends over extended time periods.

Theoretically, the precision of the technique is within millimeters, since it is basically the same as is used for precision engineering surveying. There are, however, a few practical limitations on the attainable precision. Following are a few observations about particular problems.

A possible solution to the problem of target point identification would be to climb the trees prior to the initial survey and affix permanent sighting targets at points of interest. Also, a network of similarly small definitive targets could be established throughout the sample area for use as permanent reference points, one of which could be used to define the origin of the coordinate system. A series of carefully controlled experiments should be designed specifically to determine the effects of operator error on the limits of attainable precision under different

kinds of working conditions.

Dense crown branches and foliage may place constraints on the usefulness or convenience of this method in some kinds of vegetation.

When precision is required, surveying should be avoided during periods of adverse weather conditions. Tarpaulins can be suspended over the instruments so that work may be carried on during rain or snow, but these conditions also affect visibility within the forest. Winds that are strong enough to cause movement of the trees will obviously increase the probability of meaningless apparent displacements, and should be avoided.

As of this writing, the system has been used exclusively for the dimensioning of trees. The principles upon which it is based, however, are universally applicable mathematical relations. Therefore the technique should be eminently suited to the study of a variety of ecological problems involving relations that can be described in a three-coordinate system. These might include, for example, the structure of bird rookeries, the spatial arrangement of epiphyte or parasite plants, or flower and fruit distributions.

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Estimates of biomass and fixed nitrogen of epiphytes from old-growth Douglas-fir

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Abstract

Epiphytes are sampled concurrently with measurements of surface area of trunk and branch systems of old-growth Douglas-fir (Pseudotsuga menziesii). Crude predictions of epiphyte biomass in branch systems are corrected by more detailed sampling of a subset of branch systems. Nitrogen analyses enable conversion of epiphyte biomass to the total amount of nitrogen present in the epiphytes.

Introduction

Epiphytic lichens and mosses are a conspicuous component of forest ecosystems in the Pacific Northwest. Because of their ability to concentrate materials from the environment and the ability of some of them to fix atmospheric nitrogen, their importance in nutrient cycling within the system may be greater than their contribution to total biomass would suggest.

In old-growth Douglas-fir forests, epiphyte biomass is expected to be in a steady state; epiphyte growth is balanced by litterfall, *in situ* decomposition, and consumption by herbivores. Annual turnover of epiphytic lichens varies from 5 to 25 percent (Edwards et al. 1960, Pike 1971).

Epiphyte-fixed nitrogen accounts, at least

in part, for the nitrogen needed for the growth of these epiphytes, and may represent a significant input to the forest ecosystem. Nitrogen is added to water flowing over tree surfaces through decomposition of epiphytes and leakage from nitrogen-fixing epiphytes, and enters the soil from the epiphyte system via throughfall, stemflow, and litterfall.

Measurements of biomass are necessary to relate process studies of epiphytes to their contribution to forest mineral cycles on an ecosystem level. Estimating epiphyte biomass by felling and sampling selected trees is neither possible nor desirable in old-growth Douglas-fir forests (where trees may approach 100 m in height) because such felling is destructive, not only of the host tree, but also of the epiphytes one wishes to study.

This paper outlines the methods and gives

preliminary results of techniques developed for sampling epiphytes on old-growth Douglas-fir in the H. J. Andrews Experimental Forest. The relatively nondestructive sampling is an extension of the procedure for estimating tree structure and biomass described by Denison et al. (1972).

Methods

The Study Tree

Epiphyte sampling by the methods described here has been carried out on a single old-growth Douglas-fir tree. This tree is located on a north-facing slope in watershed 10 of the H. J. Andrews Experimental Forest, 75 km east of Eugene, Oregon. The base of this 65 m tall tree is at an elevation of 500 m. The surrounding stand of old-growth Douglas-fir has an understory which includes western hemlock (*Tsuga heterophylla*) and vine maple (*Acer circinatum*). Epiphytic lichens and bryophytes are present on the understory trees and shrubs as well as the overstory Douglas-fir.

Sampling of Epiphytes

For sampling, the tree was divided into trunk(s) and branch systems. The trunk is the main vertical axis of the tree; branch systems are sets of branches leaving the trunk at the same point and are made up of axes (>4 cm in diameter) and branchlets (<4 cm in diameter).

Techniques for rigging and climbing the tree are described by Denison et al. (1972). In brief, modified rock-climbing techniques coupled with a movable spar allow access to all parts of the trunk and branch systems.

Trunk Sampling

Epiphytes were sampled from each of two climbing paths on opposite sides of the trunk. Quadrats, 1 x 2.5 dm, were placed alternately to the right and left sides of each climbing path at 1 m intervals, and cover data for epiphytes were obtained. Epiphytes for biomass estimates were cleared from one of every

four quadrats; sequential samples were taken from alternate sides of the climbing path. Ultimately, the four compass directions located at 45° from the climbing paths were sampled with equal frequency both for cover data and for biomass samples. Each 8 m high section of trunk yielded 16 sets of cover data (four from each compass direction) and four samples for biomass determinations (one from each compass direction).

Description of Branch Systems

From climbing positions on the trunk, descriptions were made of the various branch systems (length, basal diameter, number of axes, epiphyte cover, etc.). Denison et al. (1972) have discussed the processes of describing branch systems and calculating an importance value, *v*, related to total wood, foliage, and epiphyte biomass, for each branch system. Branch systems to be sampled in detail were selected with the sampling probability for any branch system being directly related to the *v* for that branch system.

The descriptive data for each branch system were also used to compute an importance value for epiphytes (EIV). EIV is a rough initial estimate of the total area (in square decimeters) covered by lichens and bryophytes on the axes within the branch system and is used to extrapolate the biomass of epiphytes on the sample branches to the entire tree. In the future, EIV (which relates to epiphyte biomass) will be used in sample branch selection when epiphytes are concerned, and not *v* (which relates to total wood, needle, and epiphyte biomass).

In computing EIV for a branch system, each axis was treated as a right cone truncated at a diameter of 4 cm. The product of the percentage cover by epiphytes and total surface area of the axes is an estimate of the total area covered by epiphytes within the branch system, exclusive of the epiphytes on the branchlets. EIV for an axis is computed by the formula:

$$EIV = \frac{C\pi(r+4)\sqrt{h^2 + (r-4)^2}}{100}$$

where C is the percentage cover by epiphytes, r is the radius at the base of the axis, and h is the length of the axis. The bulk of epiphyte biomass for these branch systems is assumed to occur on the axes; if this is not the case, the biomass of epiphytes on the many small branch systems, which are made up entirely of branchlets, may be significantly underestimated.

Since EIV is based partly on subjective estimates of length of axes and percentage cover by epiphytes, the relationship between EIV and epiphyte biomass may be expected to vary from worker to worker and from sampling period to sampling period, and for this reason will be treated separately for each tree. However, it should be possible to correct importance values so that correlations may be obtained that will hold across a set of trees.

Sampling Branch Systems

The basic sampling unit for epiphytes on axes in the branch systems is a "cylindrat," which is analogous to a quadrat but runs completely around the axis so that two edges are fused. Our 1 dm cylindrats include the entire surface for a distance of 1 dm along an axis. Thus the surface area of the cylindrat varies, depending on the diameter of the axis in the region sampled.

Cylindrats were spaced along an axis with a distance of 4 dm from the center of one cylindrat to the center of the next. The distance from the trunk to the first cylindrat sampled along a main axis was varied from 0 to 1, 2, and 3 dm so as to avoid errors which would be introduced by horizontal zonation on the axis near its origin from the trunk. Estimates of epiphyte cover were made, and then the epiphytes were stripped from the cylindrat and bagged. Axis diameter at the center of each cylindrat was measured to enable calculation of surface area of the axes.

Branchlets (<4 cm diameter at the base) were numbered consecutively in a clockwise direction within a branch system. Every fourth branchlet was cut, bagged in the canopy, and returned to the laboratory for further analysis.

Sorting and Weighing

Epiphyte materials from quadrats, cylindrats, and branchlets, were sorted by species and freed of needles, bark, and other debris. Samples were oven-dried (100° C) and weighed.

Computations

Epiphyte Biomass on Trunks

The biomass figures from quadrats of known area (2.5 dm²) can be related to the trunk as a whole once trunk surface area is calculated. Since epiphytes show a marked vertical zonation, these computations were made for short sections of trunk. It was convenient to treat the trunk as a series of truncated cones, each 4 m high; this gave two quadrats with biomass data taken from opposite sides of each 4 m high cone. Measurements of trunk diameter were made at 5 m intervals; diameters at 4 m height increments were interpolated. In the future, we plan to adjust our sampling scheme so that epiphyte biomass may be calculated on 5 m sections.

Epiphyte Biomass on Branch Systems

Epiphyte biomass on axes of the branch systems was calculated in a manner similar to that employed on the trunks. Each axis is made up of a stack of truncated cones 4 dm in length; these cones start and end in the center of the cylindrats from which epiphytes were removed. Since we know the diameters at the center of the cylindrats, we can calculate the surface area of the cones. The average weight per unit area for each species of epiphyte in the two cylindrats associated with each of these cones was used to estimate epiphyte biomass, by species, for the truncated cone. Each cylindrat was treated as the surface of a cylinder with diameter equal to the diameter at the center of the cylindrat for the purpose of calculating epiphyte biomass per dm².

Average total weight of epiphytes per branchlet, multiplied by the number of branchlets, gives an estimate of the total weight of epiphytes on branchlets within the

branch system. Total epiphyte weight for a branch system is the sum of the weights on axes and on branchlets.

Nitrogen Analyses

Samples analyzed for nitrogen content were collected in watershed 10 in August and October 1971. Samples were air dried, and nitrogen analyses were performed by Dennis Lavender of the Forestry Sciences Laboratory, Oregon State University, using the Kjeldahl method. Air drying samples analyzed for nitrogen content avoids losses of nitrogen that may occur with oven-drying. In order to enable expression of the nitrogen contents on an oven-dry-weight basis, air dried samples of epiphytes were oven-dried at 100° C to determine weight loss on drying.

Results

The results presented here are preliminary results from the first tree sampled in watershed 10 of the H. J. Andrews Experimental Forest. The estimates are crude. They are presented to give an idea of how the methodology is being applied and the order of magnitude of results that are being obtained. These preliminary results are being used in improving and refining the sampling strategy.

Biomass of Epiphytes on the Trunk

Total epiphyte biomass on the trunks of tree 1 is estimated to be 4.5 kg (table 1). Nearly 90 percent of this is bryophytes, and nearly 50 percent is found within 8 m of the ground. Lichens contribute the bulk of the epiphyte biomass on the trunk from about 50 to 60 m from the ground. Epiphyte biomass per unit area for the trunk as a whole is 0.31 g/dm², and is much higher than this figure only within 8 m of the ground and at the top of the second trunk, where large patches of *Lobaria oregana* (Tuck.) Müll. Arg. were encountered.

Biomass of Epiphytes on the Branch Systems

The frequency distribution of branch sys-

tems by EIV is presented in figure 1.

Epiphyte biomass on axes of the five branch systems sampled in detail ranged from 0 to 198 g (table 2); that on the branchlets ranged from 1 to 48 g (table 3). The five branch systems show a relationship between EIV and epiphyte biomass (fig. 2). Values from the least-squares regression line were used to convert the number of branch systems in an EIV class to an estimate of the total epiphyte biomass represented by that class (fig. 3).

The low importance value classes (EIV < 10), although representing many branch systems, make only a small contribution to the epiphyte totals for the tree. About one-half of the epiphyte biomass is contributed by branch systems with EIV above 35. In this connection, the preliminary nature of these results must again be emphasized as no branch system with an EIV higher than 32 was selected for detailed sampling.

Epiphyte Biomass for the Whole Tree

Total epiphyte biomass for the tree sampled is estimated to be 18.3 kg; 13.8 kg, or about 75 percent of the total, is on the branch systems (table 4). Assuming that the distribution of epiphyte biomass by species on the five branch systems studied is the same as the distribution overall, 50 percent of the total epiphyte biomass for the tree is bryophytes (table 4). However, there is a decrease in the proportion of total epiphyte weight represented by bryophytes from larger diameter to smaller diameter stem sections. Bryophytes make up 86 percent of the epiphyte biomass on the trunk, 47 percent of that on the axes of the branch systems (>4 cm diameter), and only 3 percent of that on the branchlets (<4 cm diameter). Nearly one-half of the *Lobaria oregana* is found on branchlets; most of the remainder is found on axes.

Standing Crop of Fixed Nitrogen

Results of nitrogen analyses show that those lichens which have *Nostoc* as their phycobiont and fix atmospheric nitrogen have

Table 1.—Epiphyte biomass on the trunk of tree 1 in watershed 10¹

Height (m)	Trunk surface area	Species											All species	
		<i>Scapania bolanderi</i>	<i>Hypnum circinale</i>	<i>Dicranum spp.</i>	<i>Sphaerophorus globosus</i>	<i>Cladonia spp.</i>	<i>Peltigera aphthosa</i>	<i>Alectoria sarmentosa</i>	<i>Platismatia glauca</i>	<i>Platismatia herrei</i>	<i>Nephroma bellum</i>	<i>Lobaria oregana</i>		
	dm ²	----- g -----											g	g/dm ²
TRUNK 1:														
0—4	1,500	300	470	340	—	+	—	—	—	—	—	—	1,120	0.75
4—8	1,240	80	210	740	—	—	—	—	—	—	—	—	1,040	.83
8—12	1,130	20	200	90	30	—	—	—	—	—	—	—	340	.30
12—16	1,110	50	150	40	20	+	—	—	—	—	—	—	270	.24
16—20	1,060	140	140	70	20	—	—	—	—	—	—	—	360	.34
20—24	1,010	20	110	10	—	10	—	—	—	—	—	—	150	.15
24—28	960	+	+	10	—	—	—	—	—	—	—	—	10	.01
28—32	900	20	60	20	—	—	—	—	—	—	—	—	90	.10
32—36	860	+	10	10	+	—	—	+	—	—	—	—	20	.02
36—40	820	200	30	50	+	+	—	—	—	—	—	—	290	.36
40—44	750	—	+	+	+	+	—	—	—	—	—	—	10	.01
44—48	670	10	110	10	—	—	—	—	—	—	—	—	130	.19
48—52	580	—	+	30	+	—	—	+	+	—	—	—	40	.07
52—56	490	—	+	+	+	—	10	50	—	—	—	—	70	.13
56—60	402	—	—	—	—	—	—	50	10	—	—	+	60	.14
60—63	250	—	—	70	10	10	+	10	—	—	—	—	100	.39
TRUNK 2:														
41—45	440	—	10	+	10	—	—	+	—	+	—	—	10	.03
45—49	310	—	60	+	20	—	—	—	—	10	—	—	90	.28
49—51	120	—	—	+	+	—	—	—	10	+	10	310	330	2.84
Total	14,610	850	1,570	1,480	120	20	10	110	20	10	10	320	4,530	

¹Weights for each species of epiphyte are to the closest 10 g; + indicates the presence of less than 5 g. Entries have been rounded and will not necessarily add to the total.

Table 2.—Epiphyte biomass on axes of branch systems sampled¹

Branch system	Section of axis			Epiphyte biomass	
	Distance from beginning of axis	Diameter at base	Surface area		
	<i>dm</i>	<i>cm</i>	<i>dm</i> ²	<i>g/dm</i> ²	<i>g</i>
7 ²					
33	0—3.5	9.0	9.62	0	0
	3.5—7.5	8.5	10.37	0	0
	7.5—11.5	8.0	9.74	.01	.1
	11.5—15.5	7.5	8.80	.02	.2
	15.5—19.5	6.5	8.17	.02	.1
	19.5—23.5	6.5	7.38	.02	.1
	23.5—27.5	5.2	6.28	.02	.1
	27.5—31.5	4.8	5.66	.02	.1
	31.5—33.5	4.2	2.59	.04	.1
Total			68.6		.9
61	0—2.5	8.0	6.28	.24	1.5
	2.5—4.5	8.0	5.34	.30	1.6
	4.5—8.5	9.0	11.00	.31	3.4
	8.5—12.5	8.5	10.21	2.50	25.6
	12.5—16.5	7.8	9.27	2.97	27.6
	16.5—18.5	7.0	4.30	1.48	6.4
	0—3.0*	4.5	4.01	.25	1.0
Total			50.4		67.1
93	0—1.5	12.0	5.54	.52	2.9
	1.5—5.5	11.5	14.14	1.13	16.0
	5.5—9.5	11.0	13.35	1.17	15.7
	9.5—13.5	10.2	11.94	.97	11.5
	13.5—17.5	8.8	11.15	1.30	14.4
	17.5—21.5	9.0	11.15	1.68	18.7
	21.5—25.5	8.8	10.52	2.03	21.4
	25.5—29.5	8.0	9.11	1.28	11.1
	29.5—33.5	6.5	8.48	1.40	11.8
	33.5—37.5	7.0	8.80	2.26	19.9
	37.5—41.5	7.0	7.39	1.38	10.2
	41.5—45.5	4.8	5.97	2.25	13.4
	45.5—49.5	4.8	5.81	2.39	13.9
	49.5—53.5	4.5	5.34	.54	2.9
	53.5—56.0	4.0	3.14	.36	1.1
	0—2.0*	6.5	4.01	.23	.9
	2.0—6.0*	6.2	7.38	.35	2.6
	6.0—10.0*	5.5	6.28	.26	1.7
	10.0—14.0*	4.5	5.34	.10	.5
	0—4.0**	4.5	5.34	1.38	7.3
Total			160.2		198.0
116	0—2.5	10.0	7.66	.04	.3
	2.5—6.5	9.5	11.50	.23	2.6
	6.5—10.5	8.8	10.56	.37	3.9
	10.5—14.5	8.0	9.55	.67	6.4
	14.5—18.5	7.2	8.61	.69	6.0
	18.5—22.5	6.5	7.67	.25	2.0
	22.5—26.5	5.7	6.72	.26	1.7
	26.5—30.5	5.0	5.78	.24	1.4
	30.5—32.0	4.2	1.93	.12	.2
Total			70.0		24.4

¹ Asterisks (*, **) denote secondary axes.² No axes greater than 4 cm diameter.

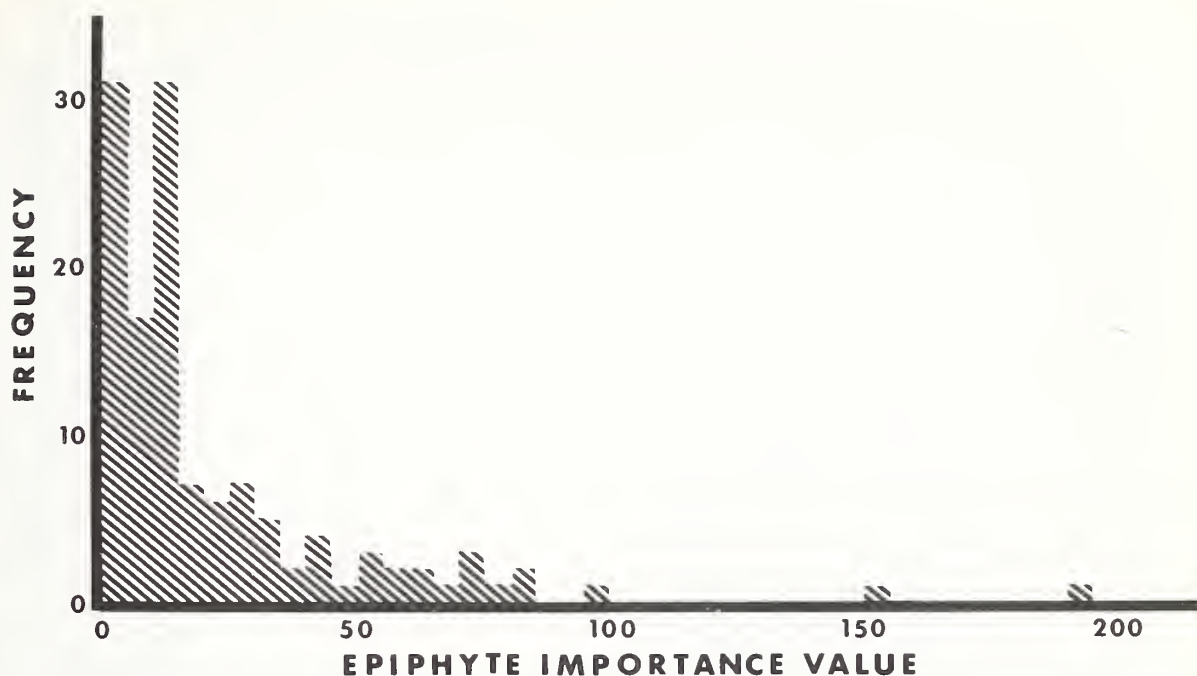


Figure 1. Frequency distribution of branch systems by epiphyte importance value. EIV is an estimate of the total area (dm^2) covered by epiphytes on the axes of the branch system.

Table 3.—Number of branchlets and epiphyte weights on branchlets for branch systems sampled from tree 1 in watershed 10

Branch system number	Number of branchlets sampled	Total weight of epiphytes on branchlet number			Mean epiphyte weight per branchlet	Total number of branchlets in branch system	Estimated total weight of epiphytes on branchlets
		1	2	3			
		-----g-----			g		g
7	1	0.40			0.40	3	1.2
33	3	.01	0.08	0.51	.20	13.5 ± 1.5^1	2.7
61	1	15.99			15.99	3	48.0
93	1	4.14			4.14	4	16.6
116	3	.14	5.62	1.72	2.48	12.5 ± 1.5^1	31.0

¹ Estimated. Total number of branchlets not recorded.

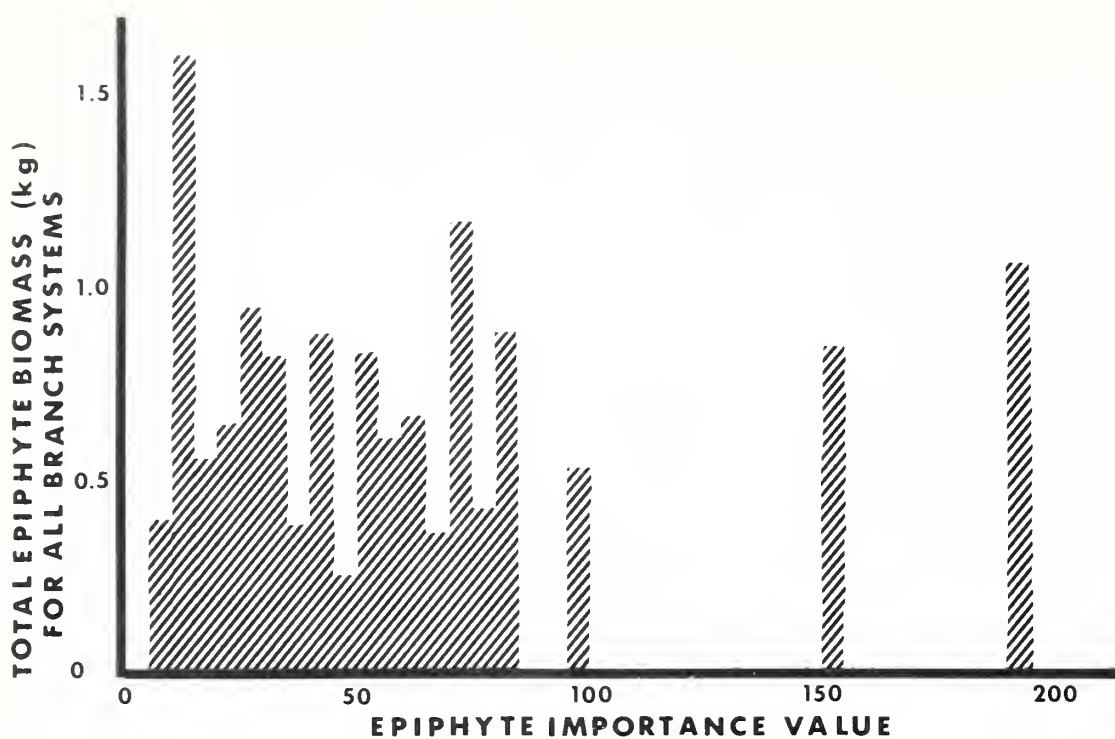


Figure 2. Relationship between epiphyte importance value and total epiphyte biomass for the five branch

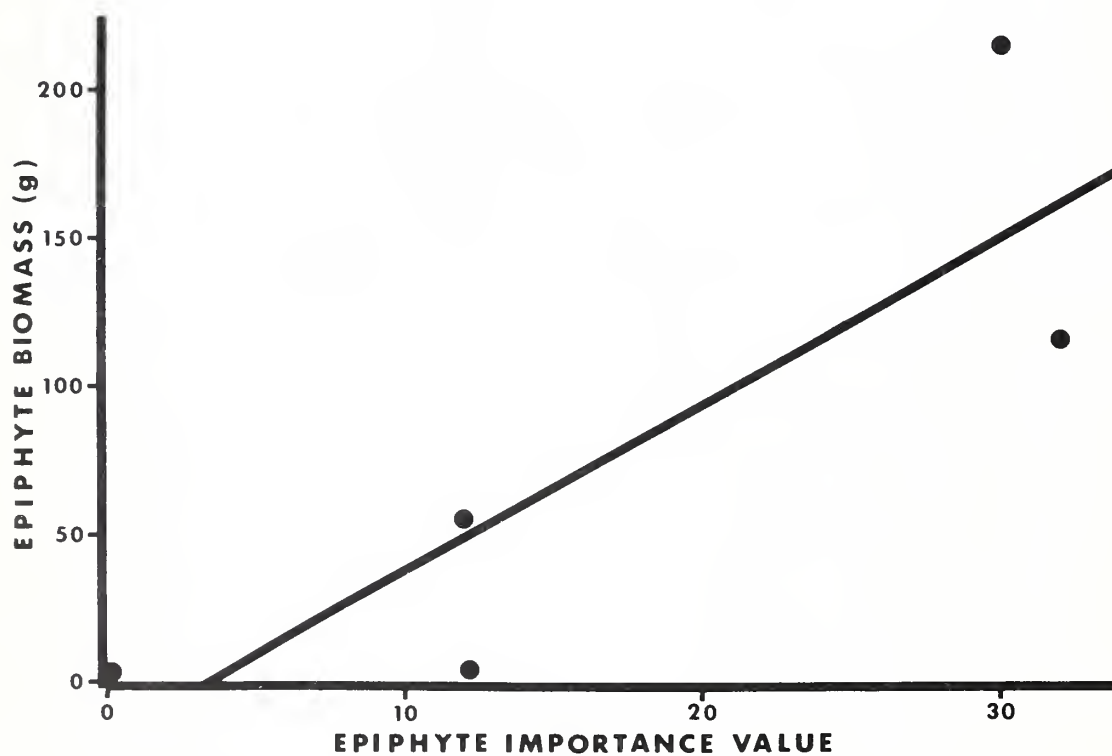


Figure 3. Estimates of total epiphyte biomass on the branch systems in each EIV class.

Table 4.—Biomass estimates (kg) for epiphytes on trunk and branch systems of tree 1 in watershed 10

Epiphyte	Trunk	Branch systems		Total
		Axes	Branchlets	
BRYOPHYTES				
<i>Hypnum circinale</i>	1.6	2.6	—	4.2
<i>Dicranum</i> spp.	1.5	1.5	—	3.0
Other mosses	—	.1	0.1	.2
<i>Scapania bolanderi</i>	.8	.1	—	1.0
Other liverworts	—	.5	—	.6
Bryophyte total	3.9	4.9	.1	8.9
LICHENS				
<i>Sphaerophorus globosus</i>	.1	1.8	—	1.9
Other lichens with green algal phycobionts	.2	.4	.3	.9
<i>Lobaria oregana</i>	.3	3.2	3.0	6.5
Other lichens with <i>Nostoc</i> phycobionts	—	.1	—	.1
Lichen total	.6	5.4	3.4	9.4
TOTAL	4.5	10.3	3.5	18.3

a much higher nitrogen content than those which do not (table 5). In two of these associations, *Lobaria oregana* and *Peltigera aphthosa* (L.) Willd., *Nostoc* is a secondary phycobiont located in cephalodia. Levels of nitrogen in the nitrogen-fixing lichens are similar to those previously reported (Pike 1971). The nitrogen contents of the mosses and nonnitrogen-fixing lichens are comparable to those reported by Rodin and Bazilevich (1967) from tundra and conifer ecosystems, but are much lower than those reported from the agricultural Willamette Valley (Pike 1971).

Using these values of nitrogen content, the biomass estimates were converted to estimates of the total quantity of nitrogen in the epiphytes on this one tree (table 6). These results indicate that 65 percent of the total epiphyte nitrogen is located in lichens and that 55 percent of the total is found in a single species, *Lobaria oregana*. Since one-half of the *Lobaria oregana* occurs on branchlets,

more than 25 percent of the epiphyte nitrogen is found there.

Discussion

Our estimate of 18.3 kg of epiphyte biomass on the one Douglas-fir tree sampled is considerably higher than the average 0.3 kg per tree found in a stand of *Picea engelmannii* and *Abies lasiocarpa* in British Columbia (Edwards et al. 1960) and the 0.4 to 1.3 kg per tree found in stands of *Pinus banksiana* and *Picea mariana* in Saskatchewan (Scotter 1962). This high epiphyte biomass is related to the tremendous size of old-growth Douglas-fir. When wet, the epiphyte load on this tree is probably three to four times the dry weight and may be a significant factor affecting branch fall. (See Barkman (1958) for water capacity of lichens and bryophytes.)

There are approximately 60 old-growth Douglas-fir trees per hectare of forest in

Table 5.—Nitrogen contents of common epiphytes in watershed 10. Analyses were performed on air-dry material; results are expressed on an oven-dry-weight basis

Epiphyte	Percent nitrogen
Lichens with green algal phycobionts:	
<i>Alectoria sarmentosa</i>	0.49
<i>Hypogymnia enteromorpha</i>	.50
<i>Hypogymnia imshaugii</i>	.66
<i>Platismatia glauca</i>	.41
<i>Platismatia herrei</i>	.50
<i>Platismatia stenophylla</i>	.52
<i>Sphaerophorus globosus</i>	.42
Lichens with <i>Nostoc</i> phycobionts:	
<i>Lobaria oregana</i>	1.93
<i>Peltigera aphthosa</i>	2.84
<i>Pseudocyphellaria anomala</i>	3.07
<i>Pseudocyphellaria anthraxis</i>	2.62
<i>Stictia weigeli</i>	3.78
Bryophytes:	
<i>Dicranum scoparium</i>	.87
<i>Hypnum circinale</i>	.95
<i>Isoetecium spiculiferum</i>	1.10

Table 6.—Estimates of the total quantity of nitrogen contained in the epiphytes on tree 1 in watershed 10

Epiphyte	Nitrogen
	<i>g</i>
BRYOPHYTES	
<i>Hypnum circinale</i>	40
<i>Dicranum</i> spp.	26
Other bryophytes	17
Bryophyte total	82
LICHENS	
<i>Sphaerophorus globosus</i>	8
Other lichens with green algal phycobionts	4
<i>Lobaria oregana</i>	127
Other lichens with <i>Nostoc</i> phycobionts	4
Lichen total	143
TOTAL	225

watershed 10 (C. T. Dyrness, personal communication). Our 18.3 kg of epiphytes per tree would then correspond to 1.1 metric tons per hectare, a figure well within the range of values reported from northern conifer forests (Edwards et al. 1960, Scotter 1962, Rodin and Bazilevich 1967). Our estimate is only for the overstory Douglas-fir trees, however, and does not take into account the considerable biomass of epiphytes that is located on understory trees and shrubs.

For comparison, our estimate of the total dry weight of needle biomass on the tree sampled is 84 kg, a figure 4.6 times as high as the estimate of epiphyte biomass.

Our finding, that a large proportion of epiphyte biomass is present on small branchlets, indicates the importance of adequate sampling of this part of the tree and demonstrates the importance of nondestructive sampling because the branchlets are particularly likely to be destroyed when a large, old-growth Douglas-fir tree is felled. Since the contribution from the branchlets is significant, EIV should be modified to include a component from the branchlets to avoid underestimating the portion of epiphyte biomass located on small branch systems.

Our methodology does not include estimates of biomass of crustose lichens or free-living algae. We have observed, even on twigs smaller than 1 cm in diameter, that cover of crustose lichens is regularly greater than 50 percent of the total surface area of the twigs. Our estimates must be considered underestimates since they include only bryophytes and foliose and fruticose lichens.

Acknowledgments

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Litter, foliage, branch, and stem production in contrasting lodgepole pine habitats of the Colorado Front Range

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Abstract

Harvest data are presented from a 70-year-old naturally thinned stand of lodgepole pine (*Pinus contorta* Dougl.) in the subalpine *P. contorta*/*Vaccinium myrtillus* habitat and from five stands of similar-aged lodgepole pine in the drier *P. contorta*/*Geranium fremontii* habitat. These latter stands include both naturally thinned and artificially uniform-thinned treatments. Stand structure, natural mortality, biomass components, growth increments of stem wood, branches, and foliage, and net primary production of these materials are given in tables. Litter production over a 4-year period is also reported for each stand; sources of variation in litter production are discussed.

Introduction

Forests of lodgepole pine (*Pinus contorta* Dougl.) are extensive in the central and northern Rocky Mountains and portions of the Cascade Range. Studies on net primary production are lacking, however, in virtually all habitats in which this pine is the major resource. Biomass studies in certain lodgepole pine habitats in Alberta have been published (Kiil 1968, Johnstone 1971), and in Colorado, the biomass of forest floor humus and pine foliage has been reported (Moir and Grier 1969, Moir and Francis 1972). These studies were not extended to net primary productivity. Our rather extensive knowledge of net stem wood production in the central Rocky Mountains (Myers 1967) does not reveal the relationship between productivity and the lodgepole pine habitats or include branch and foliage production. I report below, therefore, results of a 4-year study in Colorado concerning aspects of net primary productivity in mostly 70-year-old natural stands of lodgepole pine.

Methods

Six stands on the east slopes of the Front Range in Boulder County, Colorado, were studied. Stand LH2 occurs in the subalpine *P. contorta*/*Vaccinium myrtillus* habitat; the others occur in the drier, montane *P. contorta*/*Geranium fremontii* habitat. Habitat features and pine population statistics are given by Moir (1969), Moir and Francis (1972), and table 1. In each stand a rectangular study plot was established in an area where the forest structure appeared homogeneous. Plot size varied with stem density (table 1). Annual litter fall was periodically measured from randomized 0.25 m² microplots permanently located within each plot (Moir and Grier 1969). All surface organic material in the microplots was collected at 4-month intervals in 1969, and in late August, the remaining years. Mineral contamination at collection was minimized by computing litter

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Table 1.—Some population characteristics of *Pinus contorta* in stands on the east slopes of the Colorado Front Range

Stand and year	Age ¹	Plot area	Number of stems by d.b.h. classes							Density	Mortality
			0-2.5	2.5-5	5-7.5	7.5-10	10-15	15-20	20-25		
	<i>Years</i>	<i>m</i> ²	<i>----- cm -----</i>							<i>Stems/ha</i>	<i>Stems/ha x yr</i>
2.2	71	84									
1966			130	136	27	2				35,700	
1970			82	135	25	4				29,300	1,600
4.1	72	126									
1966			3	35	56	38	5			10,900	
1970			1	24	49	39	8			9,600	325
1.1	72	126									
1966			1	26	46	30	10			9,000	
1970				24	35	36	12	1		8,600	100
1.3	103	150									
1966			2		7	5	25	8		3,100	
1970					5	5	23	12		3,000	25
4.3	71	375									
1966			29	1	1	12	45	2		1,600 ²	
1970			25	2		7	45	8		1,650	0
LH2	77	150									
1966				2	4	10	18	19	4	3,800	
1970				2	4	9	18	20	4	3,800	0

¹ Reference year 1970. Stand age is based upon the oldest trees.

² This stand was thinned in 1934-35. Density refers to stems over 2.5 cm d.b.h.

fall as loss-on-ignition (Moir and Grier 1969), and the tendency of debris of the forest floor to "drift" into the microplots was offset by slightly increasing the effective area of the microplot during computation.

In each of plots 1.1, 4.3, and LH2 of table 1, the stems of lodgepole pine were placed into five diameter (d.b.h.) classes, with an equal number of stems in each class. In September 1969, the tree at the midpoint of each d.b.h. class was harvested (Ovington, Forrest, and Armstrong 1967), giving five trees from each plot. Current and second year foliage

and twigs were separated from each other and from older material. Branches with any living foliage whatever were classified as living and separated from dead branches at harvest time. From each stem replicate disks were obtained at the stem base, at 3 to 4 dm., and just below the lowest living branch (crown base). From each disk I measured diameter inside bark, diameter outside bark (d.o.b.), wood density (volume determined by water immersion), bark density at 102° C., and average radial growth during each of growing seasons 1968 and 1969. In addition, measurements of

d.o.b. were made at periodic lengths along the felled stems. Since this harvest procedure is not effective for estimating cone production (Ovington, Forrest, and Armstrong 1967, Lotan and Jensen 1970), this is not included in the study. Biomass values are reported at 70° C. oven-dry weights except for bole materials (stem wood and bark) which are reported at 102° C. oven-dry weights.

Stem biomass was calculated by the Smalian equation, multiplying each volume segment by the appropriate wood density observed from the disks. Stem biomass increments were computed as the difference between Smalian biomass for the years 1969 and 1968. Similarly, bark biomass for each bole was determined by the Smalian difference between diameters inside and outside bark, using bark densities for each volume segment. The increment of living branches was calculated using estimative ratios (Whittaker and Woodwell 1968), assuming that relative branch increments are approximated by relative stem wood increments. Branch mortality was computed by a canopy displacement model (Madgwick 1968). The computation assumes a canopy steady state in which the upward displacement of the envelope of green foliage within a stand leaves a wake of dead branches that were alive the previous year. The average displacement of foliage was further assumed to be the mean height growth of each stand. Stem mortality was computed from the mortalities of table 1, in which the biomass of dead stems during the mortality period was determined from the basic allometric relationship between stem biomass and d.b.h.

Calculations were based on the equations below:

Biomass and growth increments.

I. Stem.

$$W_s = k[(d_1^2 + d_2^2)\rho_1 + (d_2^2 + d_3^2)(T - 1)\rho_2 + (d_3^2 + .75^2)(H - T - 3)\rho_3]$$

$$\Delta W_s = W_s - W_{s-1}, \text{ where } W_{s-1} \text{ is obtained by substituting } d_i - 2\Delta r_i \text{ for } d_i (i = 1, 2, 3).$$

H = total stem length (ft)

T = stem length to crown
(lowest living whorl)

d_1, d_2, d_3 = diameter inside bark at ground level, 1 ft, and lowest living whorl respectively (inch).

ρ_1, ρ_2, ρ_3 = wood densities at ground level, 1 ft, and lowest living whorl (g/cc).

k = conversion constant to metric = 0.07722

$\Delta r_1, \Delta r_2, \Delta r_3$ = mean radial growth (inch) at ground, 1 ft, and crown base.

W_s = biomass (kg) at 102° C

II. Living branches.

$$\Delta W_b = W_b \frac{\Delta W_s}{W_s} + \text{new twig biomass}$$

$$\text{Branch mortality (per tree)} = W_b' \frac{(\overline{\Delta H})}{T'}$$

where $\overline{\Delta H}$ is average height growth for stand, T' is stem length within the crown over which branch mortality is observed, and W_b' is the live branch biomass along stem portion T' , W_b is total live branch biomass of the crown (along stem length H-T).

III. Basic allometric equation.

$$W = k_1 D^{k_2}, \text{ for biomass } W \text{ and DBH of } D, \text{ and regression constants, } k_1 \text{ and } k_2.$$

In the case of plot 4.3 where a clear trend of stem wood increment with d.b.h. exists, the plot increment of stem wood was computed by linear regression over the independent variable, d.b.h.

Results

Litter Production

Tables 2 and 3 give annual litter production in the six stands over the 4-year period. The mean annual litter production was 0.46

Table 2.—Annual litter fall in Colorado stands of *Pinus contorta*.
Values are given as loss on ignition weights.

Year	Stand						Total	
	2.2	4.1	1.1	1.3	4.3	LH2	Mean	Number of samples
----- kg/m^2 -----								
1967			0.46				0.47	17 ¹
1968	0.37	0.47	.36	0.63	0.30	0.38	.40	52
1969	.41	.56	.50	.88	.52	.69	.59	52
1970	.25	.39	.37	.45	.30	.54	.37	52
Mean	.34	.47	.42	.65	.37	.52	.46	

¹ A fire in our drying oven caused the loss of many samples. Only the samples from stand 1.1 entirely escaped the fire and can be used for comparison with other years.

Table 3.—Constituents of the 1967-68 annual litter fall, as loss on ignition in *Pinus contorta* stands in Colorado

Stand	Number of samples	Needles		Branches		♀ Cones		♂ Cones		Bark	
		%	kg/m^2	%	kg/m^2	%	kg/m^2	%	kg/m^2	%	kg/m^2
2.2	7	66	0.24(18) ¹	18	0.07(65)	12	0.05(59)	1	0.00(58) ²	3	0.01(20)
4.1	7	64	.30(10)	13	.06(105)	18	.08(98)	1	.00(90)	5	.02(28)
1.1	7	68	.24(11)	10	.04(29)	15	.05(52)	1	.00(45)	6	.02(36)
1.3	8	54	.34(28)	6	.04(60)	34	.21(103)	2	.01(44)	5	.03(59)
4.3	15	83	.25(17)	2	.01(105)	9	.03(72)	3	.01(35)	2	.01(70)
LH2	8	72	.26(14)	10	.04(55)	10	.04(94)	4	.02(21)	4	.01(56)
Mean	52	68	.27	10	.04	16	.07	2	.01	4	.02

¹ Coefficient of variation in parentheses.

² Trace quantities are less than 0.005 kg/m^2 . Rounding errors may cause the percentages for each stand to total around 100. Only trace quantities of nonpine debris are found in each stand.

kg./m². Both tables show, however, that numerous sources of variation in litter fall occur in lodgepole pine forests. Variation within plots is evident (table 3). Generally needle fall is less variable from microplot to microplot (CV from 10 to 18 percent except in low density stand 1.3) than other components of the annual litter production. Branches and female cones exhibit very high spatial variability, and the latter is further enhanced (beyond the values of table 3) through activities of the common pine squirrel, *Tamiasciurus hudsonicus*. Generally the percentages of needles, branches, etc. are rather uniform within and between stands, but marked departures from mean percentages are found in the low density stands 1.3 and 4.3. These departures probably result from the lessened sloughing of branches at lower portions of the bole. Thus, branches comprised only 2 percent of the annual litter fall in stand 4.3, but 18 percent in high density stand 2.2. The very high cone accumulation in stand 1.3 is partially explained by fire thinning around 1900 which removed many smaller, noncone-bearing trees, and partly by the chance distribution of collection sites near prominent cone-bearing trees. The mean annual litter fall at the bottom of table 2 indicates that stands with least canopy mass (2.2 and 4.3) have lowest litter fall, and those with greatest canopy mass (1.3 and LH2) have the highest litter fall. This relationship is not clear, however, when only a single year's annual litter fall is considered.

In all stands, 1969 was the maximum litter fall year. Nevertheless, year-to-year differences are not consistent from stand to stand. Thus, 1970 was the year of least litter production in stand 2.2 but not LH2. Seasonal variations are also significant. The inclusive period from early June to late August gave 38 percent of the total annual litter production in 1969, but only about 26 percent of the total from the same stands the following year. While some materials such as branches may be shed somewhat uniformly through the year, others such as needles showed weak seasonal peaks from June through October. In only one year was there a conspicuous "peak season" of needle fall in late August and Septem-

ber; in general, each stand was shedding needles continuously throughout the year.

Biomass and Net Growth Increments

The live components of the aboveground pine crop are given in table 4. From the data the coefficients, k_1 and k_2 , of allometric equations of the form, $W = k_1 D^{k_2}$, were computed by regression (W is biomass in kg and D is d.b.h. in cm from columns of table 4). These allometric equations and the entire population of d.b.h. values in each of plots 4.3, 1.1, and LH2 were used to compute the stand biomass values of table 5. This biomass and the mean increments of table 4 were used to compute the "new growth" values of table 6. The mean values of table 2 and the appropriate percentages of litter constituents in table 3 were multiplied to give the litter fall results of table 6. Stand LH2 in the *P. contorta/V. myrtillus* habitat is clearly the most productive. In this stand the proportion of green needles to living shoot parts is very high in average to dominant tree sizes, as shown in the last column of table 4. By contrast stand 1.1 in the *P. contorta/G. fremontii* habitat (Moir 1969) has in general a lower ratio of green needles to living shoot parts in average to dominant trees. Current year fascicles comprise a greater end-of-season proportion of the green canopy (25 to 31 percent) in stand 1.1 than in stand LH2 (17 to 27 percent). Most trees in the latter stand retain fascicles for several years longer than stand 1.1. Stand 4.3 occurs in the same habitat as stand 1.1 but was thinned in 1934-35 to about 2.5 x 2.5 m stem spacing. The consequence was to reduce light competition and encourage lateral branch growth. Surviving stems retained a high proportion of needles (11 to 17 percent of the shoot weight), and abscission would not occur until about the 5th year. By 1969 this stand had again reached a "closed" canopy condition; excess needles were abscissing as suggested by the high needle percentage of table 5 and by the negative net needle production in table 6. Further discussion of foliage characteristics of these stands is given by Moir and Francis (1972).

Table 4.—Biomass and growth increments from harvested *Pinus contorta* trees

Stand and tree		D.b.h.	Total shoot ¹	Bole ²	Stem wood		Living branches		Green needles		
					W_s	Δ/W_s	W_b	Δ/W_b	W_n	Δ/W_n	W_n/S^3
		<i>cm</i>	<i>----- kg -----</i>		<i>kg</i>	<i>%</i>	<i>kg</i>	<i>%</i>	<i>kg</i>	<i>%</i>	<i>%</i>
LH2	5	19.3	145	111.2	103.1	2.2	12.4	4.9	12.3	22	8.9
	4	16.5	91	68.0	63.1	1.4	7.8	3.3	5.8	18	7.1
	3	12.4	49	42.0	38.8	2.2	2.7	4.8	2.7	17	5.7
	2	10.0	27	23.4	21.0	1.5	1.1	3.6	1.0	27	3.9
	1	7.6	11	9.2	8.5		.7		.4		3.9
Mean						1.8		4.2		21	
1.1	5	10.0	23	17.9	16.1	1.9	1.4	5.5	1.4	25	6.3
	4	7.6	13	9.6	8.6	1.3	.8	4.5	.8	30	6.7
	3	7.6	13	10.8	9.8	2.2	.7	5.7	.8	28	6.4
	2	5.1	4	3.5	3.1	.8	.13	4.6	.16	31	4.1
	1	3.6	2	1.8	1.6		.05		.02		1.1
Mean						1.6		5.1		28	
4.3	5	14.0	44	24.2	22.5	1.7	6.5	5.1	4.9	25	12.6
	4	12.7	30	19.3	18.1	1.8	4.2	4.3	3.0	24	10.6
	3	11.7	25	17.4	15.8	1.9	3.2	5.3	2.6	27	10.8
	2	10.7	18	10.7	9.7	2.2	2.5	4.8	2.6	20	15.5
	1	8.9	15	9.0	8.6	2.3	2.0	7.5	2.4	26	17.1
Mean								5.4		24	

¹ Includes bole, living and dead branches, cones, and needles.² Stem wood plus stem bark.³ S refers to total shoot less dead branches.

Table 6 suggests that organic production and turnover in the three stands is approximately steady (Kira and Shidei 1967). The only meaningful net annual accumulation is the stem wood component (and the unmeasured root wood). Of course, my branch mortality model assumed a steady state condition for these stands, but the assumption is not disturbed in table 6 where new growth and branch mortality are balanced by the observed contribution of branches and needles to the litter fall.

The inherent photosynthetic capacity of stand LH2 is high by virtue of the great leaf biomass and surface display of current-year foliage (Moir and Francis 1972). The two stands of the drier habitat have considerably less foliage. Stand 4.3 has only half the increment of current-year foliage as stand 1.1 (table 6). Since current-year foliage has greater photosynthetic capacity than older pine foliage (e.g., Larson and Gordon 1969), this difference may account for the reduced amount of net stem wood production in stand

Table 5.—*Pinus contorta* stand biomass, 1970, from harvests on the east slopes of the Colorado Front Range

Compartment	Stand					
	4.3		1.1		LH2	
	kg/m ²	%	kg/m ²	%	kg/m ²	%
Live pine crop:						
Bole ¹	3.24	46	9.44	57	21.68	58
Live branches	.75	11	.83	5	2.11	6
Roots	1.78 ²	25 ²	4.28	26	9.68	26
Green needles	.50	7	.84	5	1.74	5
Cones	.35	5	.57	3	.24	1
Dead branches	.39	6	.57	4	1.69	4
Total	7.01	100	16.53	100	37.14	100
Standing dead timber ³	0		1.06		.15	
Forest floor humus ⁴	2.85		3.16		3.86	
Ground flora ⁵	.01		0		.005	
Total	9.87		20.75		41.18	

¹ Stem wood plus bark.

² Biomass of roots with diameters over about 5 mm were computed on the basis of nine excavated root systems. Percentages and totals in stands 1.1 and LH2 assume root biomass to be about 25 percent of the live pine crop (Rodin and Bazilevich 1967).

³ Above ground parts only (bole plus branches).

⁴ After Moir and Grier 1969.

⁵ Shoot parts only, from harvests in August 1967.

4.3 despite both stands having identical leaf area indices of 4.5 m²/m² (Moir and Francis 1972).

Conclusions

Pine stands in the Lodgepole Pine Zone of Colorado (Moir 1969) are not very productive per unit of current-year leaf biomass. It is instructive to compare the net primary productivity of stand LH2 (the most productive in this study) with pine stands having similar steady state quantities of annual foliage production. Unfortunately, there are very few published studies of net primary productivity for older natural stands of *Pinus* (Art and

Marks 1971, Kira and Shidei 1967). However, several studies within young plantations or natural stands do permit comparison, as given in table 7. It is clear that annual stem and branch production in the *P. contorta* stand is well below that of the three younger pine types. Numerous studies within developing pine plantations have led workers to conclude that within a few years after canopy closure gross productivity levels off and in following years net production declines as stand respiration continues to increase. Forrester (1969) concluded that the weight of foliage in developing *P. radiata* plantations (the oldest of his series of stands is given in table 7) is probably constant after about 12 years. However, I am not convinced on the

Table 6.—Annual turnover from certain shoot components of *Pinus contorta* stands in Colorado¹

Component	Stand		
	4.3	1.1	LH2
----- kg/m ² -----			
Bole			
New growth	0.06	0.15	0.39
Stem mortality	0	-.02	0
Net	.06	.13	.39
Branches			
New growth	.04	.04	.08
Branch mortality	-.03	-.01	-.03
Litter fall	-.01	-.04	-.05
Net	0	-.01	0
Needles			
New growth	.12	.24	.37
Litter fall	-.32	-.29	-.38
Net	-.20	-.05	-.01

¹ Litter fall is determined by the equation:
 $L_i = f_i \bar{L}$, where \bar{L} is the 3- or 4-year mean (table 2) and f_i is the fractional component of needles or branches from table 3.

Table 7.—Some comparisons of annual increments in shoot components of contrasting pine stands

Stand	Age	Density	Annual production			References
			Foliage	Stem	Branches	
	yr	stems/ha	----- metric tons/ha -----			
<i>P. contorta</i>	77	3,800	3.7	3.9	0.8	This study
<i>P. radiata</i>	12	1,560	3.1-3.3	10.8	2.9	Forrest 1969
<i>P. virginiana</i>	17	5,750	4.3	5.8	3.6	Madgwick 1968
<i>P. densiflora</i>	33	2,340	3.4	8.7	2.1	Hatiya et al. 1965

basis of the structure of the different pine crops (tables 1 and 5 and comparable descriptions from references in table 7) that the three lodgepole pine stands of this study carry appreciably greater burdens of respiratory biomass (Yoda et al. 1965). The major limitation of pine productivity in the Central and Northern Rocky Mountains may be the generally infertile soils and inimical continental climates. Under these environmental conditions not even the thinning treatment (stand 4.3) and subsequent surge of productivity in surviving stems gave increased yield on an area basis (table 6).

Management decisions in the Colorado Lodgepole Pine Zone must recognize the inherent low productivity of *P. contorta*. Where wood production must continue to have management priority, efficiency of utilization can be increased at least 10 percent if live branches can be economically included in the harvest (table 5) (Young 1968). Management can also be directed toward uneven-aged stands for purposes of esthetics, enhanced groundcover production, or better game utilization. Small, irregularly shaped clearcut areas are also an attractive management possibility for long-term planning in this low productivity region. This study suggests strongly that because of its very low productivity, especially when compared against the productivity of intensively managed pine plantations, lodgepole pine stands in environments of site index of 90 or less should be regarded as only minor resources of wood harvest. A greater percentage of such land in the lodgepole pine region of North America might be devoted to recreational usage.

A much neglected management tool in lodgepole pine forests is prescribed burning. Periodic fires were an important feature of lodgepole forests (Moir 1969). This study and others (Kiil 1968) reveal that high quantities of slowly decomposable materials build up within natural stands. Fairly high quantities of nutrients become locked up in the forest floor humus (Moir and Grier 1969); this humus together with the shaded condition of the forest floor in closed stands has adverse effect upon the ground flora (Basile and Jensen 1971, Moir 1966). Controlled fire has

at least four possible beneficial effects in lodgepole pine forests: (1) The reduction of fuel and wildfire probability, (2) stimulation of ground vegetation, (3) a nutrient "pulse" effect stimulating tree production, (4) tree thinning and conversion to uneven-aged stands. The possible use of controlled surface fires in *P. contorta* should be given considerably more attention.

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Small mammal and bird populations on Thompson site, Cedar River: parameters for modeling

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Abstract

Preliminary estimates of small mammal and bird populations on the Thompson site in the Cedar River watershed were made from 1969 to 1971. Mammal populations were estimated through a kill-trap grid, and bird populations through systematic direct observations. The small mammal fauna, notably rich in insectivorous forms, has as its most abundant members Trowbridge shrew (*Sorex trowbridgei*), vagrant shrew (*Sorex vagrans*), shrew-mole (*Neurotrichus gibbsii*), Oregon vole (*Microtus oregoni*), and deer mouse (*Peromyscus maniculatus*). Bird populations differed between summer and winter. In the summer the most abundant species were Swainson's thrush (*Hylocichla ustulata*), winter wren (*Troglodytes troglodytes*), Oregon junco (*Junco oreganus*), black-throated gray warbler (*Dendroica nigrescens*), chestnut-backed chickadee (*Parus rufescens*), brown-headed cowbird (*Molothrus ater*), and MacGillivray's warbler (*Oporornis tolmiei*). In winter only two birds were common: winter wren and golden-crowned kinglet (*Regulus satrapa*). For these species estimates were obtained for abundance, biomass and, for the mammals, energy flow.

Introduction

This paper represents a first step in providing the information on terrestrial vertebrates which will be needed in the development of ecosystem models for the Western Coniferous Forest Biome. It covers the initial investigations on small mammal and bird populations, which have centered on the Thompson site of the Cedar River watershed, King County, Washington. Consideration is given to methodology, results in terms of species populations, ecological role, biomass and energy, and the desirable directions for further investigations.

The Thompson site consists of a second-growth Douglas-fir (*Pseudotsuga menziesii*) forest about 60-70 years old, on Barneston soils formed from glacial outwashes. Elevations vary from 210-310 meters. There are

small variations in ecological conditions within the forest, as indicated by differences in the understory vegetation.

Every biotic community is composed of individual species, and these must be identified and studied individually in building up knowledge concerning the whole. Schwarz (1967, p. 225-226) outlines our task and its difficulties as follows:

In order to determine the role of the species in the energy metabolism of the ecosystem, we must, first of all, determine with the necessary reliability the following parameters of the population: the absolute numbers of animals; their biomass; the structure of the population (because the intensity of the matter and energy metabolism of animals of different weight, sex, age, physiological

condition differ); the turnover rate of the population, and the intensity of metabolism of different groups of animals . . . Whilst it is not difficult to estimate the intensity of metabolism of certain species in a calorimetric chamber, it is practically impossible to estimate the loss of energy by a bat, a mole, or a dolphin in the process of their natural life activity.

In the light of these considerations we will examine our preliminary data and, through a comparison of actual and needful information, delineate the work still to be done.

Small Mammal Studies

Since small mammals are generally inconspicuous, and do not make readily detectable signs, the determination of species presence and especially population density is widely recognized as a difficult problem.

The most commonly used method for estimating population densities in small mammals is to capture, mark, and release a sample, and then capture a second sample containing both marked and unmarked individuals. Several underlying assumptions (Leslie 1952) are: all individuals have equal probabilities of capture, released individuals disperse randomly into the populations, and there is no mortality, natality, or significant ingress or egress during the experimental period.

Since these assumptions were not warranted in our case, and since we needed to collect specimens for data on weight, food habits, and reproduction, we considered intensive removal methods. Grodzinski et al. (1966) proposed such a method for IBP small mammal studies. They suggested intensive kill-trapping following a prebaiting period on a defined grid of locations. This provided data for an estimation procedure in which a regression line, plotted for the number of animals caught each day (on the ordinate axis) against the cumulative number previously caught, would provide an estimate of population density (the point where the regression line intersected the abscissa). Earlier work on this

approach was that of DeLury (1947), Hayne (1949), and Zippin (1958).

The major flaw in the method of Grodzinski et al. (1966) is that it gives no accurate estimate of the area sampled by the grid, because the small mammals move some unknown distance to the trapping point. Since the area sampled is not defined, population densities cannot be determined.

Adamczyk and Ryszkowski (1968) suggested that the sample grid be surrounded on each side by an external belt of trapping locations to catch animals moving toward the inner grid before they could reach it, thereby controlling the "periphery effect."

The data provided by the external trapping belt cannot be used, because the distance travelled by each animal before being caught is highly variable (Miller 1970).

Adamczyk and Ryszkowski (1968) recommend a 5-day prebaiting period to accustom the mammals to the trap locations, followed by a 5-day period of removal trapping. Their basic assumptions are: (1) all residents of the inner grid are captured, (2) prebaiting does not increase the resident density, and (3) individuals not resident on the inner grid are not captured on the inner grid; immigrants and individuals resident in the outer grid will be captured, if at all, in the outer grid.

Of these three assumptions, we could test only the second. Adopting a 5-day prebaiting period, we ran pairs of trap-lines—one prebaited and one control—in each case. Total catches over 5 days were not different, though prebaited lines took a higher proportion of the catch on the first day (Miller 1970). This finding corroborates that of Babinska and Bock (1969), who showed that prebaiting did not significantly increase the density of resident small mammals.

Our trapping procedure was as follows: a 5.94-ha (12.4-acre) sample area was divided into 256 stations, 16 rows by 16 lines, with 15.2-meter spacing. Anchored at each station was a paper plate which was baited with oatmeal, millet, sunflower seeds, oats, and wheat for 5 days. Then the remaining bait was removed and two mouse traps were placed on each plate, one trap baited with a peanut butter-bacon grease mixture, and the other

with a birdseed-Crisco mixture. Traps were run for 5 full days.

Two such grids were established to sample the range of variability within the Thompson site, and each was trapped twice, once in summer and once in winter, as follows: Grid I: July 22 to 27, 1969, and March 22 to 27, 1970; Grid II: September 6 to 11, 1969, and February 18 to 23, 1970. The results (table 1) show several patterns. There is a difference between summer and winter populations in almost all cases as well as a number of differences between plots. From other work on small mammal populations we would predict that there would also be variations from year to year.

Since this method assumes that all the mammals on the inner grid are caught, it is important that trapping be highly efficient. Study of the trapping data (Miller 1970) suggests that winter populations may not be as trappable as summer populations, so winter estimates in table 1 may be low. We have planned further work to increase trapping efficiency and so improve the accuracy of these estimates.

Meanwhile, it is possible with our present data to obtain at least preliminary values for small mammal biomass (table 2). Note that the differences between the two plots in total biomass are rather small, and that the drop from summer to winter, in total biomass, is

Table 1.—Small mammal density estimates from grid-trapping (number per hectare)

Species	Grid I		Grid II	
	July	March	September	February
<i>Sorex trowbridgei</i>	16.8	3.0	8.2	3.0
<i>S. vagrans</i>	4.3	2.6	1.3	.4
<i>Neurotrichus gibbsi</i>	3.5	.9	3.6	1.3
<i>Microtus oregoni</i>	1.3	.9	1.7	1.7
<i>Peromyscus maniculatus</i>	1.7	1.3	2.2	1.3
Total	27.6	8.7	17.0	7.7

Table 2.—Small mammal biomass (grams per hectare)

Species	Grid I		Grid II	
	July	March	September	February
<i>Sorex trowbridgei</i>	82.3	18.5	41.0	16.5
<i>S. vagrans</i>	27.4	17.8	6.7	2.7
<i>Neurotrichus gibbsi</i>	27.9	7.7	51.4	11.1
<i>Microtus oregoni</i>	19.8	14.1	28.6	27.9
<i>Peromyscus maniculatus</i>	27.7	22.0	36.6	22.2
Total	185.1	80.1	164.3	80.4

proportionally about the same for each plot. Future studies will tell us what fractions of this biomass are attributable to various nutrient substances; that is, what the chemical constitution of these small mammal bodies is.

We can already make preliminary estimates of energy flow through these small mammal populations. The initial energy source for ecosystems is sunlight. It is fixed by green plants and may be passed to populations of plant-eating animals. Within animal populations energy is used in respiration and tissue production and may also be passed on to other (predatory) animal populations. Much less energy is expended in tissue production than respiration.

We can combine published data on the

caloric value of animal tissue and on small mammal metabolic rates with our estimates of biomass and information on population dynamics to estimate the energy consumed in tissue production and respiration for our small mammal populations.

The energy incorporated in tissue production, for small mammals, has been estimated to average 1.5 kcal/gm (Gorecki 1965). The energy expended by the animal in its daily activity—the metabolic rate—varies by species. The values used in our calculations are given in table 3.

We do not as yet have a detailed knowledge of the dynamics of these small mammal populations. However, we now know enough to establish upper and lower limits of energy

Table 3.—Metabolic rates used in calculating the energy expended in respiration by small mammals

Species	Cal/gm/day	Authority
<i>Sorex trowbridgei</i>	806	Pearson (1948)
<i>S. vagrans</i>	920	Pearson (1948), Gebczynski (1965)
<i>Neurotrichus gibbsi</i>	800	Authors' estimate
<i>Microtus oregoni</i>	500	Estimate based on value for red-backed vole (Pearson 1947)
<i>Peromyscus maniculatus</i>	440	McNab (1963)

Table 4.—Estimated energy flow (respiration + tissue production) through small mammal populations (kcal per hectare per year)

Species	Minimum	Maximum
<i>Sorex trowbridgei</i>	5,250	15,750
<i>S. vagrans</i>	3,470	7,420
<i>Neurotrichus gibbsi</i>	2,760	6,810
<i>Microtus oregoni</i>	4,300	6,430
<i>Peromyscus maniculatus</i>	4,450	6,860
Total	20,230	43,270

flow for these species by using data on reproduction, seasonal population density and growth of young (Miller 1970). These estimates are given in table 4. If necessary, we can strive for more accuracy in future estimates through a more detailed knowledge of the dynamics of these populations.

The role and foraging stratum of mammals in the forest ecosystem can be roughly categorized as shown in table 5. Secondary consumers are relatively numerous in the small

mammal populations pointing to the abundance of their invertebrate foods in the litter and soil of the forest.

In categorizing such roles, we must recognize that the primary consumers do on occasion eat other animals, and that the secondary consumers do eat plants. It remains for us to delineate in more detail the nature of the seasonal diet for each species, as well as the rates of consumption, and the amounts and composition of the excretory products.

Table 5.—Names, foraging strata, and consumer roles of mammals of the Thompson site, Cedar River watershed, Washington

Scientific name	Common name	Foraging stratum ¹	Consumer role ²
<i>Canis latrans</i>	Coyote	G	II°
<i>Cervus canadensis</i>	Elk (wapiti)	G,S	I°
Chiroptera	Bats	C	II°
<i>Eutamias townsendi</i>	Townsend's chipmunk	G,S	I°
<i>Lepus americanus</i>	Snowshoe hare	G,S	I°
<i>Lynx rufus</i>	Bobcat	G	II°
<i>Microtus oregoni</i>	Oregon vole	G	I°
<i>Mustela erminea</i>	Shorttail weasel	G	II°
<i>Mustela frenata</i>	Longtail weasel	G	II°
<i>Neotoma cinerea</i>	Bushytail woodrat	G,S	I°
<i>Neurotrichus gibbsi</i>	Shrew-mole	B,L	II°
<i>Odocoileus hemionus</i>	Black-tailed deer	G,S	I°
<i>Peromyscus maniculatus</i>	Deer mouse	L,G	I°
<i>Sorex trowbridgei</i>	Trowbridge shrew	L	II°
<i>Sorex vagrans</i>	Vagrant shrew	L	II°
<i>Tamiasciurus douglasi</i>	Chickaree	G,S,C	I°
<i>Ursus americanus</i>	Black bear	L,G,S	I°
<i>Zapus trinotatus</i>	Jumping mouse	G	I°

¹B = soil layer; L = litter layer; G = ground layer, under 1 foot; S = shrub layer, 1 to 6 feet; C = crown layer, area occupied by living crowns of forest overstory.

²I° = primary consumer, eats mostly plant material; II° = secondary consumer, eats mostly animal matter.

Bird Studies

The forest birds were sampled both summer and winter on a 6.0-ha plot chosen to represent the Thompson site. This plot was divided into fifteen 0.4-ha sample units on a map of the whole plot. A series of transects was made through the whole plot on each sample day by Erickson who noted each bird observation by location and species. During the summer sample period (May and June), many breeding males were singing, which facilitated their detection. During the winter observation period (December), there had to be more dependence on sight than sound.

Five days of observation were spent at each season, and all observations took place during mornings when there was no heavy rain. The results for the two seasons are given in table 6.

Some less common, but in some cases rather large birds, are also found on the Thompson site. During the coming year we will be able to make population estimates of these species, adding substantially to our total estimate of bird biomass.

The contrast between summer and winter populations is much sharper for birds than for small mammals. This has implications for ecosystem modeling, since some birds reproduce on the Thompson site but winter elsewhere, presumably suffering some mortality, and thus constituting a one-way movement of energy and nutrients out of the Thompson site. From a knowledge of body weights we have calculated the biomass of common birds on the Thompson site by season (table 6).

Energy-flow estimates for these bird populations cannot yet be made because neither population estimates of the larger birds nor annual cycles of abundance of each bird species are yet available for the Thompson site. This must be one of our next topics of study.

The role and foraging stratum of birds is roughly categorized in table 7. As in the case of small mammals, some of these birds shift seasonally in their consumer-roles. A diet of invertebrates is essential for the young of all species. Also, shifts in the relative abundance of available food will presumably be reflected in food habits. These are also topics on which more work must be done.

Table 6.—Abundance (number per 100 hectares) and biomass (grams per hectare) of the most common birds by species and season

Species	Abundance		Biomass	
	Summer	Winter	Summer	Winter
<i>Molothrus ater</i>	26	0	11.4	0
<i>Junco oreganus</i>	43	0	9.9	0
<i>Troglodytes troglodytes</i>	36	33	3.5	3.1
<i>Hylocichla ustulata</i>	16	0	5.8	0
<i>Dendroica nigrescens</i>	43	0	4.5	0
<i>Parus rufescens</i>	23	0	2.3	0
<i>Regulus satrapa</i>	0	33	0	2.0
<i>Oporornis tolmiei</i>	26	0	1.6	0
Total	213	66	39.0	5.1

Table 7.—Names, foraging strata, and consumer roles of birds of the Thompson site, Cedar River watershed, Washington

Scientific name	Common name	Foraging stratum ¹	Consumer role ²
<i>Bombycilla cedrorum</i>	Cedar waxwing	C	I°
<i>Bonasa umbellus</i>	Ruffed grouse	L,G,S,C	I°
<i>Bubo virginianus</i>	Great horned owl	G	II°
<i>Colaptes cafer</i>	Red-shafted flicker	G,C	II°
<i>Columba fasciata</i>	Band-tailed pigeon	L,S,C	I°
<i>Corvus brachyrhynchos</i>	Common crow	G	II°
<i>Corvus corax</i>	Common raven	G	II°
<i>Dendragapus obscurus</i>	Blue grouse	L,G,S,C	I°
<i>Dendrocopos villosus</i>	Hairy woodpecker	S,C	II°
<i>Dendroica nigrescens</i>	Black-throated gray warbler	S,C	II°
<i>Empidonax</i> spp.	Empidonax flycatchers	S,C	II°
<i>Hylocichla ustulata</i>	Swainson's thrush	L,G	II°
<i>Ixereus naevius</i>	Varied thrush	L,G	II°
<i>Junco oreganus</i>	Oregon junco	L,G	I°
<i>Loxia curvirostra</i>	Red crossbill	C	I°
<i>Molothrus ater</i>	Brown-headed cowbird	G	I°
<i>Oporornis tolmiei</i>	MacGillivray's warbler	S,C	II°
<i>Parus rufescens</i>	Chestnut-backed chickadee	S,C	II°
<i>Passerella iliaca</i>	Fox sparrow	G	I°
<i>Perisoreus canadensis</i>	Gray jay	G,C	II°
<i>Pipilo erythrophthalmus</i>	Rufous-sided towhee	G	I°
<i>Piranga ludoviciana</i>	Western tanager	S,C	I°
<i>Regulus calendula</i>	Ruby-crowned kinglet	C	II°
<i>Regulus satrapa</i>	Golden-crowned kinglet	C	II°
<i>Selasphorus rufus</i>	Rufous hummingbird	G,S	I°
<i>Sitta canadensis</i>	Red-breasted nuthatch	S,C	II°
<i>Sphyrapicus varius</i>	Yellow-bellied sapsucker	S,C	I°
<i>Spinus pinus</i>	Pine siskin	C	I°
<i>Troglodytes troglodytes</i>	Winter wren	G,S	II°
<i>Turdus migratorius</i>	Robin	L,G	II°
<i>Vermivora celata</i>	Orange-crowned warbler	S,C	II°
<i>Vireo gilvus</i>	Warbling vireo	S,C	II°

¹ B = soil layer; L = litter layer; G = ground layer, under 1 foot; S = shrub layer, 1 to 6 feet; C = crown layer, area occupied by living crowns of forest overstory.

² I° = primary consumer, eats mostly plant material; II° = secondary consumer, eats mostly animal matter.

Further Studies

The data provided for small mammal populations will be more useful if we are able to make more accurate population density estimates and if we determine the yearly, seasonal, and geographical fluctuations in density. Further, a more detailed understanding of population dynamics will permit a more accurate estimate of energy flow, and set the stage for studies of uptake, storage, and loss of chemical materials by small mammal populations.

Of course, the same sort of information must be obtained for the large mammals, which include several important primary consumers. For large mammals the role of movement must be studied, since seasonal movements entail a translocation of materials, and patterns of mortality provide loci of nutrient release.

For birds the study of movements will also be important, since long-distance annual migrations provide a potential mechanism for the annual loss of materials from the ecosystem.

A prime consideration in all such studies will be the establishment of confidence limits for the data, and estimates of additional sampling necessary for results of a stipulated level of accuracy. Then we will be in a position to respond to the needs of modeling in a realistic way with regard to the actual field or laboratory work which provision of any particular piece of information will require.

In addition to these inventories of vertebrate animals in the forest ecosystem, we will seek an understanding of the effects that animal populations may have on the populations of plants which constitute their food, i.e., the control function exerted by animals over plant populations. A knowledge of such relations, properly quantified, will help provide the basis for models of the dynamics of plant populations.

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Terrestrial Process Studies

Terrestrial process studies in conifers: a review

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Abstract

A few studies on the physiological processes of conifers go back as much as a century, but most information has been accumulated during the past 40 years. These efforts have involved most of the widely distributed species to some extent, but limited information is available even on those species most studied, and very little on the remainder. With Douglas-fir (*Pseudotsuga menziesii*), the most studied species of our region, considerable information is available, but insufficient for process modeling. Of other species of the Western United States much less is known. Thus intensive studies of physiological processes will be necessary in the Coniferous Biome effort on each of the species of principal importance. In this paper, the current status of information on the following topics is reviewed: CO₂ assimilation and respiration; transpiration, water conduction and water deficits; translocation of photosynthates; and mineral nutrition. Stomatal behavior and leaf resistance are considered with respect to the various gas exchanges. Energy budgets, nutrient cycling, growth, and modeling of processes are closely related to the foregoing topics, but are covered elsewhere in this symposium.

Introduction

Central in the goals of the IBP is the measurement of productivity and production, and particularly the understanding and prediction of these for vegetation and ecosystems. It follows that a basic knowledge of the physiological and related processes involved is essential to reaching these goals. In the Coniferous Forest Biome our concern is naturally centered around the conifers, although associated deciduous and herbaceous species are also important. However, this review concentrates on the conifers as the species demanding our principal efforts.

Experimentation with conifers, which began about a century ago and was taken up by various workers periodically, has been included in several general reviews in the Encyclopedia of Plant Physiology (Leyton 1958,

Huber 1956, Stålfelt 1956, Pisek 1960), and discussed in detail by Kramer and Kozlowski (1960). Since then, a number of reviews concerning woody plants have covered various aspects: viz. food relations (Kozlowski and Keller 1966), mineral nutrition (Baule and Fricker 1967), and translocation (Zimmermann and Brown 1971). Of course, the results of many experiments with broadleaved woody plants are pertinent to conifers. Further, general principles established with herbaceous plants may be applicable to conifers, although this carryover is more tenuous and in each case usually demands experimental verification.

This review will concentrate on findings of the past decade which, together with the work discussed in the reviews mentioned above, serves as the background on which the studies of the Coniferous Biome are based. Included is considerable unpublished material

from theses. The principal processes and subjects which will be covered in sequence are (A) assimilation of CO_2 and respiration, (B) transpiration, water conduction, and water deficits, (C) translocation of photosynthates, and (D) mineral nutrition. Stomatal status and leaf resistance are considered in relation to various aspects of gas exchange. Energy budgets, nutrient cycling, growth, and modeling of processes are considered by other authors in this symposium, so are not emphasized in this paper.

Assimilation of CO_2 and Respiration

The principal emphasis in the IBP on assessment and understanding of dry matter production naturally focuses attention on photosynthesis and the conditions and factors which influence its rate. Likewise the magnitude of respiratory losses is of complementary interest. Both short-term and long-term influences on the rates of these processes are of importance in estimating seasonal and annual totals. Further, both inter- and intra-specific variability must be taken into account. Regardless of the factor under study, methods of individual measurement assume marked importance, and carrying over these measurements commonly made on portions of the plant to the entire forest stand is even more important. The latter aspect is considered in the papers of this symposium on terrestrial modeling.

Measurement

The appearance in late 1971 of the detailed and authoritative book, *Plant Photosynthetic Production, Manual of Methods* (Šesták, Čatský, and Jarvis, eds.), makes a detailed consideration of principles and techniques of measurement unnecessary here. Thus a general consideration of methods and their applicability in the Coniferous Biome will suffice.

Many useful studies have been performed under controlled-environmental conditions, using assimilation chambers of various types

(Jarvis et al. 1971). Such studies may be criticized on the basis that plants grown or held for study in controlled-environment rooms or boxes may behave differently from material growing under natural conditions. Thus a number of studies have been devoted to gas exchange of conifers in the field (e.g., Botkin, Woodwell, and Tempel 1970; Gentle 1963; Helms 1965, 1970; Hodges 1967; Hodges and Scott 1968; Künstle 1971; Ungerson and Scherdin 1965; and Woodman 1971). Also the extensive unpublished studies on *Picea abies* (L.) Karst of W. Koch¹ and of O. L. Lange and E.-D. Schulze² should be mentioned. To eliminate the influence of greenhouse or controlled-environment on the plants, several workers have used seedlings or saplings brought in from the field or garden, or made measurements on excised branches from field growing trees (Brix and Ebell 1969; Keller 1971; Parker 1963; Pisek, Larcher, Moser, and Pack 1969; Pisek and Kemnitzer 1968; and Poskuta 1968).

All of the measurements in the studies cited in the previous paragraph were made using assimilation chambers of various kinds. Difficulties and potential errors associated with use of such enclosures are well covered by Larcher (1969a) and Jarvis et al. (1971). The major concerns pertain to excessive boundary layer resistances if stirring is inadequate, to significant departures of irradiation and energy balances from those of unenclosed foliage, and to errors inherent in the measuring itself.

Techniques other than those using assimilation chambers are available (Larcher 1969a, Denmead and McIlroy 1971). Harvest techniques give direct measurements of dry matter accumulation, but must pertain with conifers to time intervals of several weeks or months. Thus they cannot give information on responses to various controlling factors, nor do they give information on respiratory losses. However, apart from their intrinsic value, they may serve as an independent check on

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² Botanical Institute II, University of Würzburg, Germany.

the validity of extrapolating from assimilation chamber measurements to forest stands. Thus Botkin, Woodwell, and Tempel (1970) noted that values of production calculated from assimilation chamber data were about 30 percent above harvest values for the Brookhaven oak-pine forest. Meteorological techniques have been applied to conifer stands in a few cases (Baumgartner 1969, Denmead 1969, Kinerson 1971). These can give values for entire stands without the influence of enclosures, but require large even stands, level topography, and uniform atmospheric conditions, thus measurement of either short or long term influences of factors affecting assimilation is very difficult. The use of meteorological data in combination with physiological information has potential for mathematical modeling and prediction of CO₂ assimilation (Reed and Webb 1972).

Difficulties arise in defining and measuring the surfaces active in reception of light and in CO₂ exchange. The general problems and techniques for these assessments, particularly in relation to broad-leaved plants and grasses, are covered in the review of Květ and Marshall (1971). The needle leaves of conifers usually have longitudinal rows of stomata on the lower surface or on the interior surfaces in fascicled species. Thus it is common to consider the "one-side" area as accounting for most of the gas exchange. Areas can be attained by tedious linear measuring and counting methods (Květ and Marshall 1971, Madgwick 1964), but often dry weights of foliage only have been reported to avoid this time-consuming effort. The introduction of the glass-bead technique (Thompson and Leyton 1971) should encourage the determination of surface areas as well as dry weights so that data can be compared between species. Further, because of the mathematical relations of gas diffusion and leaf resistances, most models of photosynthesis require that values of photosynthesis be expressed on a unit leaf area basis (Reed and Webb 1972). The foliar distribution in crowns and stands must be obtained for extrapolation of gas exchange data, and several descriptions of such methods are available (Stephens 1969, Kinerson 1971).

Factors Affecting CO₂ Assimilation and Respiration

In general, the principle of limiting factors will apply to the relative importance of the environmental and endogenous variables which control photosynthetic and respiratory rates. Thus in consideration of an individual variable or factor, its effect may be masked at particular times by the limiting influence of another factor. In the discussions of any individual factor which follows, it is implicit that the influences described are those of the factor when it is believed to be limiting the metabolic process (Stålfelt 1960).

Light Intensity

Numerous studies in controlled-environmental systems and using excised branches have shown that conifers exhibit typical limiting-factor response to light, with saturation dependent on the species and growing conditions (Pisek 1960). For those species of principal interest in the Coniferous Biome a number of values for saturating light intensity have been reported (table 1). These values are in general agreement with the range of 1,850-3,200 ft-c stated by Polster (1967b) to give maximal net photosynthesis in both broadleaved and coniferous trees, except for the value quoted by Künstle (1971). Further verification of light responses under field conditions are needed for adequate modeling even of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Western hemlock, *Tsuga heterophylla* (Rafinesque) Sargent, *Pinus ponderosa* Laws., and the *Abies* species are much in need of further study with respect to light.

Recent studies on photorespiration and its enhancement with increasing light intensity in spruce species (Poskuta 1968, Ludlow and Jarvis 1971b) indicate the need to understand the variations of this process in the species of special interest in the Coniferous Biome. This information will not be necessary for our earlier empirical models, but will become essential for more theoretically based models in the future as well as being necessary for estimates of gross productivity.

Table 1.—Saturating light intensities for net photosynthesis in various species of conifers

Description of plant material	Saturating light intensity	Author
--- foot-candle ¹ ---		
Douglas-fir (<i>Pseudotsuga menziesii</i> (Mirb.) Franco):		
65-day-old seedlings grown with 1,100 ft-c long day; temp 19°C day, 9°C night	3,000	Krueger and Ferrell, 1965
100-day-old seedlings grown at 18°C and 1,000 ft-c	2,500	Brix, 1967
1-year-old seedlings—outdoor grown	ca. 2,300	Krueger and Ruth, 1969
4-year-old seedlings grown in cans in the garden	2,000-3,000	Fry, 1965
2-year-old seedlings—nursery grown	1,600	Hodges, 1965
Current year foliage from 10-year-old trees (upper crown July-Aug.)	ca. 4,600	Künstle, 1971
Western hemlock (<i>Tsuga heterophylla</i> (Rafinesque) Sargent):		
2-year-old seedlings—nursery grown	1,400	Hodges, 1965
1-year-old seedlings—outdoor grown in light shade	2,300	Krueger and Ruth, 1969
in heavy shade	1,250	
Noble fir (<i>Abies procera</i> Rehd.):		
2-year-old seedlings—nursery grown	2,000	Hodges, 1965
Sitka spruce (<i>Picea sitchensis</i> (Bong.) Carr.):		
1-year-old seedlings—outdoor grown in light shade	2,300	Krueger and Ruth, 1969
in heavy shade	1,250	
2-year-old seedlings—nursery grown	1,400	Hodges, 1965
3- to 4-year-old seedlings and branches from 10-year-old forest trees	1,450-1,930	Ludlow and Jarvis, 1971b

¹ 1 foot-candle (ft-c) = 10.8 lux; 6,750 ft-c \cong 1 cal cm⁻² min⁻¹; 1 Wm⁻² = 1.43 x 10⁻³ cal cm⁻² min⁻¹.

Temperature

The concomitant responses of respiration and gross photosynthesis to temperature, modification by light and moisture regimes and adaptation, as well as special influences of low and high temperatures, all make it difficult to clearly indicate the influence of temperature alone on these processes (Kramer and Kozlowski 1960, Kozlowski and Keller 1966, Larcher 1969b, Polster 1967b). Thus Pisek and his collaborators (1969) quoted rather considerable ranges of optimal temperatures at 10,000 Lux for a list of European species. The total ranges for the conifers in this list extended from 9° to 22°C, with the

means showing a much narrower range of 12° to 15°C. Larcher (1969b) assembled data on summer temperature optima for some 18 conifers. These varied from the low range of 12°-16°C for *Pinus cembra* L. to the high range of 20°-22°C for *Abies balsamea* (Mill.).

Data for species of our special interest in the Coniferous Biome are not abundant. For Douglas-fir seedlings values of 20°-25°C at saturating light (Krueger and Ferrell 1965), and 18°-20°C at 1,000 ft-c (Brix 1967) have been reported. For 10-year-old saplings of this species growing in the garden we noted a somewhat lower range of 12°-17°C.³ This

³ R. B. Walker and D. J. Salo. Unpublished data.

may be explained by the observation of Brix and Ebell (1969) that dry matter production of Douglas-fir shoots in bud dormancy had a broad optimal range of 12° to 24°C, with maximum increase in stem diameter and in total plant dry weight at 18°C.

Respiration is believed to follow the van't Hoff Q_{10} relationship up to about 60°C, where enzyme inactivation ensues. This is supported by measurements of dark respiration, and by the fall off in net photosynthesis above 20°-25°C (Pisek 1960, Larcher 1969b). Studying current-year needles of 10-year-old Douglas-fir, Künstle (1971) found the Q_{10} of respiration of fully expanded needles to be about 2.2, but to be about 4.0 in buds in late spring. Also Brix and Ebell (1969) noted a steady decline in dark respiration of Douglas-fir needles with years of age. However, more intensive study of respiration not only of needles but of non-green parts will be needed in our Biome effort for modeling production. This is even more pertinent for the species other than Douglas-fir.

Since the evergreens may function throughout the year, special interest has long existed in their responses to low temperatures (Pisek 1960). The low-temperature compensation points for conifers in the winter are in the range of -5° to -8°C, which is also the expected range of freezing of the needles (Larcher 1969b). Again considering species of special interest in the Coniferous Biome, the low-temperature compensation point for Sitka spruce proved to be -5°C (Ludlow and Jarvis 1971b). Respiration is very low at temperatures below 5°C, and in our climate such temperatures usually predominate only when light intensities are very low. Thus with light often limiting, temperature influences on photosynthesis are small, and net assimilation in Douglas-fir was near the maximum for short times even at 0°C if illumination was less than 500 ft-c (see footnote 3). However, the assimilation rate declined if a temperature under 2°C was maintained for an hour or more.

Wintertime depressions in photosynthetic capacity have been studied frequently in the past (Pisek 1960). These declines have been attributed to a combination of stomatal

closure and a probable biochemical factor (Parker 1963), to stomatal closure in *Picea abies*, *Pinus sylvestris* L., and *Juniperus communis* L. in northern Sweden (Ungerson and Scherдин 1965), to a breakdown of the photosynthetic apparatus in *Pinus taeda* L. (Perry and Baldwin 1966), to a reversible effect associated with freezing of the needles and presumed dehydration in *Abies alba* Mill. (Pisek and Kemnitzer 1968), to adverse needle water relations (Żelawski and Kucharska 1967), and to a typical seasonal behavior in pines (McGregor and Kramer 1963). Seasonal variations will be considered in more detail in a subsequent section.

There is some information on high temperature compensation points of photosynthesis, although nothing pertaining particularly to species of Western United States. The six European conifers studied at Innsbruck (Pisek et al. 1968) varied from 46° to 50°C in heat resistance, and from 37° to 41°C in the maximum temperature for net photosynthesis. If our species fall into similar ranges, as seems likely, there is little reason to be concerned with this aspect because only very occasionally would air temperatures reach the compensation value for photosynthesis in our region. Only if leaf temperatures should greatly exceed air temperatures on hot days would this be a matter of interest.

Carbon Dioxide

Under favorable conditions of light intensity, temperature and moisture, carbon dioxide concentration may sharply limit photosynthesis. Thus Koch (1969) reported some threefold increase in yield of several conifers from raising CO₂ concentration to 5X the normal atmospheric level in controlled environment experiments. Also Fry (1965) recorded a measurable increase in net assimilation of Douglas-fir saplings when he increased CO₂ from ambient (0.035 percent) to 0.05 percent if light intensity was above 1,600 ft-c. Likewise Ludlow and Jarvis (1971b) found that net photosynthesis of Sitka spruce seedlings increased almost linearly with CO₂ concentration as it was varied from 0 to 0.04 percent, then continued to rise less steeply to

at least 0.06 percent CO_2 . However, in the forest it is not feasible to increase CO_2 concentration except for the natural contributions from the soil and litter. It is important to make periodic checks in the field using increased CO_2 in assimilation chambers to detect if the ambient CO_2 concentration is limiting, and to minimize the "draw down" of CO_2 in enclosures to avoid excessive deviations from assimilation rates of the unenclosed foliage. Also the atmospheric CO_2 concentration is known to be variable, and this should be monitored for taking into account any limiting effect on photosynthesis.

Water Deficit

A substantial literature documents the reductions in CO_2 assimilation in various species caused by even moderate water deficits (Kozlowski and Keller 1966). Some reduction may occur in the afternoon with high transpirational rates even on well-watered soils, but lowered soil moisture is the principal cause of severe reductions. Using 4-year-old Douglas-fir saplings in containers, Fry (1965) found that depletion of bulk soil water to a potential of -5 bars reduced net photosynthesis to zero (compensation point) and reduced respiration to about 10 percent of normal. Since needle water potential dropped to about -30 bars, soil water potential at the root surfaces was probably considerably below -5 bars. Hodges (1965, 1967), studying 2-year-old Douglas-fir seedlings in the field, found net assimilation closely correlated with leaf water potential. Using 7- to 9-year-old saplings of about 0.5-0.75-m height, Hinckley (1971) found net assimilation in *Abies amabilis* (Dougl.) Forbes and *Abies procera* Rehd. to drop sharply with reduced water potential (pressure chamber method) of the needles, reaching 10 percent of maximum assimilation at about -10 bars needle water potential in the *A. procera*, and at about -13 bars in the *A. amabilis*.

Such declines in net assimilation caused by reduced soil moisture and lowered leaf water potential are well recognized to be caused by increases in stomatal and other leaf resistances (Fry 1965, Slatyer 1967, Slavík 1971, Jarvis

1971). Considerable information has been accumulated on stomatal behavior in Douglas-fir (Fry 1965, Reed 1968, Phillips 1967), ponderosa pine⁴ (Lopushinsky 1969), and true firs (Lopushinsky 1969, Hinckley and Ritchie 1970). However, meager information is available on actual values for stomatal and other leaf resistances in species of special interest in the Coniferous Biome. Fry (1965) calculated stomatal resistance in Douglas-fir saplings from stomatal infiltration pressures. From these pressures ranging from 0.25 to 1.65 atm he calculated stomatal resistances of 2.3 to 32 sec cm^{-1} for CO_2 , and additional leaf resistances of 3.7 to 83 sec cm^{-1} . Reed (1972) found general agreement with these values. Ludlow and Jarvis (1971b) reported stomatal resistances in Sitka spruce seedlings in excess of 20 sec cm^{-1} at very low irradiance or at very low temperatures, with normal values of about 4 sec cm^{-1} . Their data showed mesophyll resistances of 20 to 30 sec cm^{-1} or more at very low irradiances and at very low temperatures, with normal values of about 6 to 8 sec cm^{-1} . Leaf resistance is such an important factor that understanding stomatal and other components of resistance in all species of special interest in the Biome is necessary for the development of reasonable models of photosynthesis and transpiration.

Mineral Nutrition

A number of experiments have established that mineral deficiency may limit photosynthesis (Kozlowski and Keller 1966, Baule and Fricker 1967). In the Pacific Northwest, nitrogen deficiency is common in forests, thus making determination of the influences of this element very important in the Coniferous Biome program. The stands at the Cedar River Watershed show incipient N deficiency, so care will be taken to assess the influence of this element. Keller (1971) recently reported a 50 percent increase in CO_2 assimilation in needles of *Picea abies* seedlings with increase in N content from 0.41 to 1.11 percent. Also Brix (1971) recently measured increases in

⁴A. P. Drew, L. G. Drew, and H. C. Fritts. Unpublished data.

net assimilation in excised branches from 24-year-old Douglas-fir trees which had been fertilized with N. However, the increases were noted only at light intensities of 2,000 ft-c and above.

Diurnal and Seasonal Patterns (including adaptation)

Diurnal cycles or fluctuations in light, temperature, water vapor pressure gradients, and other external factors are interactive with internal factors such as endogenous rhythm of stomatal behavior, recovery from water deficit, and translocation. Therefore the response of a tree day by day is very complex.

Gentle (1963) and Helms (1965) studied diurnal responses of 38-year-old Douglas-fir in detail over a 4-year period. Superimposed on the daily responses to light and darkness were short-term and longer term fluctuations attributable to varying temperature, radiation and cloud cover, relative humidity, water deficit, and undetermined influences. Midday depressions were common in the summer but also occurred in cool autumn weather. Similar detailed studies of diurnal behavior of the other species important in the Biome are lacking.

The diurnal endogenous changes in stomatal aperture have been studied in several species. Fry (1965) noted that saplings grown from seed gathered at Pack Demonstration Forest, La Grande, Washington, did not exhibit any closing of the stomata during the day or night if water status was favorable. This was largely confirmed by Reed (1968), although he observed a slight closing tendency at night. Phillips (1967) studied 38-year-old Douglas-fir trees at Pack Demonstration Forest and found that the stomata of leaves in the lower crown closed at night. A geographic or provenance difference in stomatal response of Douglas-fir was demonstrated in the field in southern Oregon, where stomata were open at night in the spring and early summer, but closed at night from July through September (Reed 1972). Drew, Drew, and Fritts (see footnote 4) and Lopushinsky (1969) independently observed that the stomata of *Pinus ponderosa* are closed at night. *Abies amabilis*

growing in the field was observed to have more open stomata in early morning than did *Abies procera*, indicating that the stomata of *A. amabilis* were probably more open during the night (Hinckley 1971). The stomatal behavior of western hemlock is unknown and needs attention.

The influence of season of the year has already been touched on in connection with winter depression of assimilation. In a more general context, seasonal patterns of CO₂ assimilation were studied by Gentle (1963) and by Helms (1964, 1965) in the 38-year-old Douglas-fir stand mentioned above. As would be expected, winter assimilation was low and quite variable, depending on the light and temperature prevailing. Spring and autumn performances were good, although somewhat below the summer. Higher temperatures presumably made respiration a good deal higher in the summer than in spring and autumn and particularly than in the winter. Also Woodman (1968, 1971) studied net assimilation in one of the trees of this same stand during the growing season of 1967. A somewhat different pattern can be expected in conifers growing in regions with very dry summers, with much of the yearly total of photosynthesis occurring during the winter and spring.

Such studies of seasonal patterns are imperative for adequate models of production in forest stands. This is particularly true because a considerable number of variables in addition to those of the physical environment have marked influences (Kozlowski and Keller 1966). These include morphological variation (sun and shade foliage, stomatal distribution, cuticular thickness, and others), adaptation with respect to light intensity and temperature in particular, interspecific and intraspecific variations, shading, dormancy, age of foliage, position in the crown, and the nature of past seasons. Some information on these features is available for Douglas-fir. However very limited knowledge, gained mostly from studies with seedlings, is available in this connection for the other species of special concern in the Coniferous Biome program—western hemlock, ponderosa pine, and one of the true firs (Hodges and Scott 1968, Krueger and Ruth 1969, Ludlow and Jarvis 1971b,

Pharis et al. 1967). Again Helms (1970) has studied CO₂ assimilation in ponderosa pine during the summer in the natural environment, and envisions extending this study to all seasons of the year. Intensive work on CO₂ assimilation of all of the other species named above from the standpoints of environmental factors and the other influences on their behavior will be needed for realistic modeling of their photosynthetic production.

Water Relationships

Although water deficit was taken up in the previous section as a potential limiting factor in CO₂ assimilation and respiration, the general subject of water relationships is of concern in water balance, nutrient cycling, and other soil-plant-atmosphere relations, as well as in its effects on plant metabolism. Also the balance between water absorption and transpiration determines any water deficit in the plant. Water relationships of woody plants were thoroughly reviewed by Polster (1967a).

Water Absorption

The factors affecting water uptake in woody plants were discussed in detail in Kramer and Kozlowski (1960). In the usually well-drained and well-aerated soils of the western forests, temperature of the soil and roots and the level of soil moisture are the principal factors affecting water uptake in the root zone. These factors are being regularly monitored at the intensive study sites of the Biome. Their influence will be of most concern in the magnitude of water deficits. Since water uptake is wholly passive during times of high water use, increased resistance to uptake in the root zone can be expected to enhance water deficits. Further, rate of water uptake and conduction may exert some effect on mineral uptake (Slatyer 1967). Investigations of water uptake will probably not be a part of the Biome studies, because of the difficulties of measuring this quantity in large soil-rooted plants, and the near equivalence of absorption rates to transpiration rates.

Water Conduction

For woody plants, this aspect has been thoroughly reviewed, including special features of conifers, by several authors (Huber 1956, Kramer and Kozlowski 1960, Zimmermann and Brown 1971). With reference to the objectives of the Coniferous Biome, interest in conduction pertains to the magnitude of negative sap pressures (as a measure of water deficit), to its use as an indicator of transpirational fluctuations where actual transpirational measurements can not be made readily, to intra-tree water adjustments including potential storage in stems and branches, and to its influence on rate of translocation of mineral nutrients. Nonetheless, rates of conduction will be inferred of necessity for our models from transpirational rates. However, some indication of the nature of potential storage of water in stems or branches may be attained from measurements using sap velocity flow meters and by study of intra-crown variation in the sap pressure (Scholander technique) (Waring and Cleary 1967) of stems and needles (Hinckley 1971, Ritchie 1971).

Transpiration

The predominant interest in water relationships is with transpiration both from a hydrologic viewpoint concerned with total plant use, and from its influence on water deficits and on resistance to water vapor and CO₂ transfer. This major interest has resulted in substantial work on the transpiration of conifers, and considerable attention to species of interest in the Coniferous Biome. These studies will be considered below under the headings of measurement, influence of environmental factors, effects of leaf temperature and resistances, and the significance of water deficits.

Measurement

Although there are various methods for measurement of transpiration, in the field with large plants the air-flow method using leaf enclosures, lysimeter systems, meteorological techniques, and tritiated water methods are most feasible. The air-flow

method, using psychrometers or infra-red gas analyzers as the detecting instruments, is commonly applied to plant material enclosed in assimilation chambers. The possible artifacts of the systems pointed out for CO₂ assimilation measurements (Jarvis et al. 1971) are even more critical in the case of transpirational assessments. This is true because of the role of energy balance and resulting leaf temperature in determining the vapor pressure gradient from leaf to atmosphere. Also adsorption and condensation problems often make measurements difficult and less accurate during cool moist periods either diurnal or seasonal, although rates are characteristically low under such conditions. The lysimeter technique is suited to diurnal and seasonal studies without the artificiality of enclosing the foliage (Fritschen 1972). Root disturbance occurs in installation, but this should have little effect on transpiration and passive uptake of water. Meteorological methods, which measure evapotranspiration, also maintain natural conditions around the foliage, but necessitate sizable stands of homogenous vegetation and uniform air conditions for best measurements. The tritiated water method (Kline et al. 1972) yields information on transpirational activity only over periods of hours and days, but its advantage over the other methods lies in its applicability to very large trees, such as the 75-m-tall old-growth Douglas-firs in the H. J. Andrews Experimental Forest. During certain periods of 1972, all four of these methods of transpirational measurement will be compared at the Thompson Research Center (Cedar River). The lysimeter study will be continuous throughout the 1972 spring through autumn season, and the simultaneous measurement of transpired water in the gas stream from the assimilation cuvettes will permit estimation of leaf resistance as well as giving data on transpirational rates.

Influence of Environmental Factors

General discussions of these factors and their influences have been given by Stålfelt (1956), Kramer and Kozłowski (1960), and Kozłowski and Keller (1966). Emphasis here

will be on more recent studies with conifers and especially with species of special concern in the Coniferous Biome.

The dominant influence of the vapor pressure gradient from leaf to air on transpirational rate when stomata are open has long been recognized. This was verified by Ritchie (1971) in a study with *Abies amabilis* and *A. procera* of about 14-m height, using vapor pressure gradient and also saturation deficit of the atmosphere. On a statistical basis, the latter value accounted for 56 percent of the variation in transpirational rate on a seasonal basis.

Depletion of soil moisture has also long been recognized as a major factor in the control of transpiration. This was verified by Müllerstaël (1968) using three species of pine, as well as other evergreens, and he also showed marked species differences. Hinckley (1971) showed great reduction in transpiration (sap velocity) in *Abies amabilis* and *A. procera* with soil water depletion. Reed (1972) developed a computer simulation of transpiration in the field. He showed that low vapor pressure gradients limited transpiration in the spring, but increased stomatal resistance resulting from depleted soil moisture and water deficits limited transpiration during the summer. He also showed that the available soil moisture can vary greatly from year to year, which can cause considerable seasonal and annual differences in total transpiration.

Although moderate air movement is commonly recognized as a factor which increases transpiration because boundary layers are reduced, few studies have been conducted with high air velocities. Tranquillini (1969) varied wind velocity from 0.5 to 20 m sec⁻¹, and observed that net assimilation of *Pinus cembra* increased somewhat up to about 4 m sec⁻¹, then declined. In *Picea abies* the decline started at 1.5 m sec⁻¹. Caldwell (1970), working with the same *Pinus cembra* plants, showed that stomatal aperture and transpiration rate were only slightly reduced by high wind speeds, but photosynthesis was reduced considerably because of changes in needle display to the light. High wind would be expected to be of importance in the Coniferous Biome only in extreme habitats.

Effects of Leaf Temperature and Leaf Resistances

Leaf temperature establishes the vapor pressure of water in the intercellular spaces of the leaf, thus it is imperative to have good measurements of this value to accompany transpirational (and net assimilation) estimations. Methods for determination of leaf temperature have been recently described in detail (Perrier 1971).

Although transpirational rates may approach potential evaporation with favorable soil and leaf water status, commonly leaf resistances markedly impede water loss. This was well demonstrated by Waggoner and Turner (1971) in a study of transpiration in *Pinus resinosa* Ait. with both natural and artificially induced stomatal closure markedly reducing transpiration. The separation of stomatal and other leaf resistance is very desirable when feasible (Jarvis 1971). The influence of wax in the stomatal pores in reducing transpiration in Sitka spruce was noted by Jeffree et al. (1971). Similar wax accumulations increasing with age of needles in Douglas-fir have recently been observed on material collected from the 35-year-old trees at the Thompson Research Center (Cedar River).⁵ In the Coniferous Biome studies, more information is needed on these resistances in all species for successful production models.

Significance of Water Deficits

Conifer species differ in their ability to maintain photosynthetic production in the presence of water deficits, and in their ability to control water loss under similar environmental conditions (Hodges and Scott 1968). The status of woody plants can be assessed over the season by periodic tests of the predawn pressure chamber value (Waring and Cleary 1967), and this used in establishing moisture gradients and ecological tolerances and distributions. In the Coniferous Biome such assessments are needed throughout the growing season over wide geographic areas

with all species of primary interest, and this program is already well under way (Waring et al. 1972).

Translocation of Photosynthates and Relations to Growth

The translocation of photosynthate in woody plants was thoroughly reviewed by Kozlowski and Keller (1966), and very recently discussed in detail by Zimmermann and Brown (1971).

Among the conifers the pines, especially *Pinus resinosa*, have received the greatest attention (Rangnekar et al. 1969, Dickmann and Kozlowski 1970). The former group, working with 15-year-old trees in a plantation, found that each branch appeared to be self-supporting, contributing more liberally to its own growth than to the tree leader, which probably expands in part from reserve carbohydrates. Further, they suggested that the products of cambial growth are largely derived from current photosynthate. The results of Dickmann and Kozlowski (1970), who labeled the 1-year-old needles of second-order branches of 20-year-old trees, are in general agreement with this, as they found that recovery from the various sinks was high and in the order: 2d-year cones > terminal needles > lateral needles > terminal internode > lateral internodes > 1-year-old wood.

Ross (1972) labeled different-aged branch segments of 9-year-old Douglas-fir trees of about 6-m height. He likewise was able to discern source-sink relationships. The proportion of $^{14}\text{CO}_2$ exported from needles was a function of their age, of the attractive "pull" of external sinks, and inversely of water stress. One-year-old needles exported a larger proportion of their photosynthate than did current-year needles even late in the growing season. The attractive "pull" of the sinks decreased in the order: elongating new 1st-order internodes and needles, elongating new 2d-order internodes and needles, and stem. The fact that 1-year-old needles mainly supplied adjacent new shoots and thus ex-

⁵ P. Machno and K. L. Reed. Unpublished data.

ported little photosynthate basipetally in contrast with the preferential translocation of photosynthate toward the stem by 2-year-old needles may be explained by the ability of a sink such as the stem to mobilize photosynthate falling off with distance in an approximately logarithmic manner.

These studies give clues to the relationships between CO₂ assimilation in the leaves and the formation and differentiation of new cells in apical and cambial growth. These relationships are not simple, and care must be taken to avoid oversimplified connections. For example, net assimilation rates can give an index of amounts of photosynthate available for growth only if position and age of the foliage studied are taken into account (Ross 1972). With caution, however, net assimilation rates taken in different parts of the crown can be used to estimate daily mean assimilation and the total photosynthate production, on the basis of the whorls of branches of different heights (Woodman 1968, 1971).

In the Coniferous Biome studies, efforts must be made to bring together net assimilation, translocation, and terminal and lateral growth into a workable model. It may be necessary in such efforts to take into account growth inhibitors and promoters in such a model, since Lavender and Hermann (1970) have pointed out the importance of these substances in their studies of light and photo-period effects in Douglas-fir. Although there is information to build on with respect to red pine and Douglas-fir (see above), further work will be necessary with Douglas-fir to utilize the information effectively. Clearly, specific studies of translocation and growth in western hemlock, ponderosa pine, and a true fir are needed.

Mineral Nutrition

A number of books cover the general field of mineral nutrition and specifically that of forest tree species (Baule and Fricker 1967, Bengtson 1968, Epstein 1972). The aspects of particular concern in the Coniferous Biome are mineral uptake and cycling, and the role

of mineral elements in metabolic processes.

Mineral cycling studies in second-growth Douglas-fir forests have been carried out for over a decade (Grier and Cole 1972). Mineral cycling is important in the nutrition of the trees since limited nutrient capital is available. These studies need to be extended to the other species of special importance in the Coniferous Biome program.

The importance of nitrogen in chlorophyll production and the close correlation between chlorophyll contents and CO₂ uptake were pointed out by Keller and Wehrmann (1967) with reference to *Picea abies* and *Pinus sylvestris*. The widespread occurrence of nitrogen deficiency in Douglas-fir in western Washington and Oregon (Gessel et al. 1965) gives reason for careful attention to this element in studies of coastal Douglas-fir in the Coniferous Biome. Also it will be wise to make a sufficiently broad spectrum of mineral analyses to detect low levels of other elements which might be limiting photosynthesis or growth.

The foregoing indicates that a large background of information on terrestrial production processes in woody plants is already available. With respect to Douglas-fir, the species currently receiving most emphasis in the Coniferous Biome, the background is appreciable and useful, but often lacking in specific data needed for the construction of mathematical models. These deficiencies must be made up for adequate modeling of processes in this species. With other species of special concern in the Biome—western hemlock, ponderosa pine, and true firs—much more background information as well as specific data is needed in order to develop effective production models.

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Criteria for selecting an optimal model: terrestrial photosynthesis

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Abstract

In theory, there exists an infinite number of models of a given system. These models differ in resolution, scope, descriptive and predictive power. Because the models described in the literature generally reflect the personal perspectives and goals of the researchers who developed the models, it is helpful to be able to evaluate the potential of a given model to provide the information needed in another research problem. Several criteria for selection of models or modeling approach are suggested in this paper. The use of the criteria is illustrated by discussion of several mathematical models of photosynthesis taken from the literature. The models discussed include a linear regression model, an energy budget model, and models based on theory of enzyme kinetics and gas exchange.

Introduction

A great many models are available that describe photosynthesis, some of which will be discussed below. Because of the many models now available, we had hoped that we would not have to develop a new model—that we need only choose or modify an existing model. Thus it was necessary to consider certain criteria by which to judge the applicability of a given model to the purposes of the IBP.

Several of the criteria will be discussed below. This list is probably not complete, but is suggested as a guide to model selection, modeling approach, or both. Because most scientists are modelers in a broad sense, this discussion is intended primarily for those scientists who are least familiar with formal aspects of modeling.

Criteria for Model Selection

Because plant growth and presumably community composition are greatly influenced by photosynthetic capacity, that phenomenon has been the object of a great deal of study. Photosynthesis is only one component of the biochemical system resulting in plant growth. Failure to consider other factors in growth, as well as the fact that photosynthesis can be uncoupled from growth, results in the general failure of attempts to predict growth from photosynthesis. However, a model of photosynthesis is an important component of a growth model and because the process of photosynthesis is a physical-chemical system, attempts to model photosynthesis should be consistent with some basic tenets of systems theory as well as physical reality.

Systems

A system, as defined by Klir (1969), is imposed upon an *object*—a segment of nature (the earth, a community, a tree, an automobile, a computer)—by the observer from a distinct point of view. Everything that does not belong to the object is the *environment*. The boundary between the object and its environment cannot be clearly defined; thus the delimitation of the object is somewhat arbitrary and reflects the personal perspectives of the modeler. Because we usually cannot study an object in its entirety (because of its complexity), we observe or measure *values* of certain *quantities*. The choice of quantities to measure depends on what we consider to be of interest or important to the given purpose (Klir 1969).

Most scientists are familiar with the concept of a system, especially as it is applied in thermodynamics. For example, the laws of thermodynamics were derived by studying idealized *closed* systems in equilibrium. In dealing with such closed systems it is possible to study independent *state variables* such as pressure, temperature, and volume, which define the *state* of the system. A closed thermodynamic system can exchange heat and work but not matter with its environment (Daniels and Alberty 1967).

As Ludvig von Bertalanffy (1969) pointed out, biological systems are *open* systems whose structure is maintained by energy, information, and matter flow through the systems. The behavior of the system is the result of the interactions of the elements of the system and the flow through the system. Because the thermodynamic system is closed and idealized, and because the state variables are *independent* (i.e., one can be varied without affecting another), it is convenient and correct to describe the system in terms of total differentials; for example, the relation of internal free energy, E , of a system to temperature and volume, T and V , can be expressed (Daniels and Alberty 1967):

$$E = f(T, V)$$

$$dE = \left(\frac{\partial E}{\partial T}\right)_V dT + \left(\frac{\partial E}{\partial V}\right)_T dV \quad (1)$$

Equation 1 implies that the variables E , T , and V are independent; one can be varied while the others are held constant, but more importantly, equation 1 implies *summativity* in the system where the behavior of a summative system is the physical sum of the behavior of the parts. Because this approach is useful in thermodynamics and other special areas, biologists often attempt to explain observed phenomena by assuming that the elements of all systems are independent (von Bertalanffy 1969). We in plant physiology have accepted as a standard procedure the isolation of a plant in a growth chamber, and the study of the response of the plant to one factor while holding the others constant. This approach is epitomized by Cleary (1970) who derived the following model of photosynthesis:

$$P = f(M, T, L, N, Pr)$$

then

$$dP = \left(\frac{\partial P}{\partial M}\right)_{T, L, N, P} dM + \left(\frac{\partial P}{\partial T}\right)_{M, L, N, P} dT + \dots + \left(\frac{\partial P}{\partial Pr}\right)_{M, T, L, N} dPr \quad (2)$$

where P = photosynthesis, M, T, L, N , and Pr are moisture, temperature, light, nutrition and preconditioning effect, respectively. This model assumes a summative system analogous to a closed thermodynamic system.

This assumption is not totally valid in a biological system like photosynthesis. Light, for example, has an effect not only on the photochemical reactions within the leaf, but also is converted to heat, which influences leaf temperature. Likewise, leaf temperature is affected by transpiration rates, which is in turn affected by temperature, moisture status of the leaf and air, and so on, but equation 2 does not account for these interactions. While this model is inadequate in that respect, Cleary (1970) does recognize that photosynthesis is not a simple light-and-temperature related phenomenon but represents a complex interaction of diverse factors, all of which should be taken into account in order to fully understand the process. Some of the factors listed by Cleary (1970) probably are independent, namely, Pr and N .

Von Bertalanffy (1969) calls nonsummative systems *Gestalten*; for example, the non-additivity of mixing equal volumes of concentrated sulfuric acid and water. Von Bertalanffy provides another simple example where he points out that the voltage of three isolated conductors would be different from that if they were interconnected. Biological quantities often act very much like the charge in von Bertalanffy's example in that their values in concert are different from their isolated values. Thus, it is essential for a biological researcher to understand the distinction between *summative systems* and *Gestalten*. It is advisable to consider a biological system to be a *Gestalt* unless it can be proved otherwise.

We do not believe that the concepts of systems can be overemphasized. It is not necessary for each researcher to be adept at formulating systems models, but he should be aware that few things in a biological system operate independently, and that it is difficult if not impossible to understand biological phenomena if we simply take the one factor—one response approach. As a result, in modeling biological systems, the single most important concept is that the model must be a system model, consistent with the concepts of systems theory.

Theoretical Validity

We view a model as a tool to aid in understanding and prediction. Because there are, in theory at least, an infinite number of models that can apply to a given system, we must select that model which provides the greatest understanding and predictive power within certain limitations. If our system of interest can best be explained by physical principles, then the model should have physical validity, but there are systems which are not explainable from the physical paradigm, for example, animal behavior. In other cases, the physical theory is inadequate and the approach may be fruitless.

Given a physical-chemical system, like photosynthesis, a physically valid model is usually a good choice. As an almost trivial example, photosynthesis, P , has been expressed by Chartier (1966) as a function of light:

$$P = \frac{aL}{1 + bL} \quad (3)$$

where a/b is P at light saturation, and a is the slope of the curve (fig. 1) at zero light since $a = dP/dL(1 + bL)$. Lommen and coworkers (1971) express the same phenomenon as:

$$P_m(L) = \frac{P_{mL}}{1 + K_L/L} \quad (4)$$

where P_{mL} is photosynthesis at light and CO_2 saturation and K_L is that light intensity at which $P_m(L) = 1/2 P_{mL}$ (fig. 2).

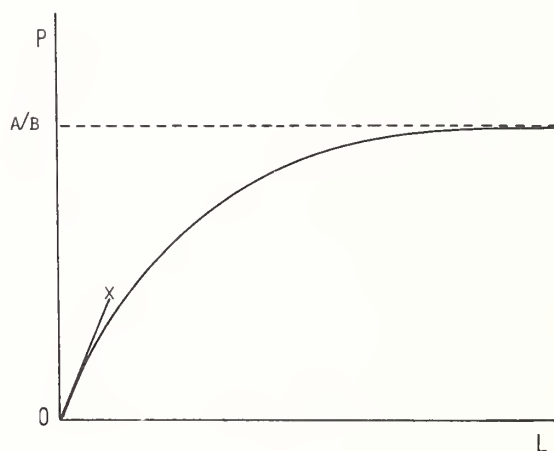


Figure 1. Photosynthesis as a function of light. From Chartier (1966) A = slope of line O,X . Description in text.

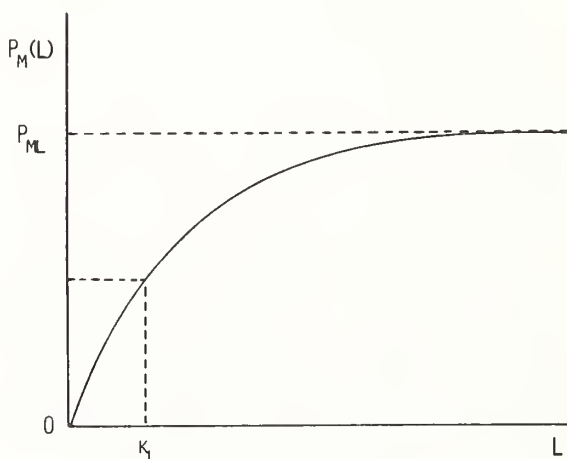


Figure 2. Photosynthesis as a function of light. From Lommen et al. (1971). Description in text.

It is obvious that in essence equation 4 is identical to equation 3, where $P_{mL} = a/b$ and $K = 1/b$. Both models describe the light dependence of photosynthesis equally well; one model is not more complex than the other. Yet, we would choose equation 4 because the parameters have more physical meaning. The curve could also be described by:

$$P = \beta_0 + \beta_1 L + \beta_2 L^2 + \beta_3 L^3 \dots \quad (5)$$

which has even less appeal because it is nearly impossible to determine the physical meaning of the parameters (β_i).

It could be argued that equation 4 is little more valid than equation 3. Equation 4 is derived from the Michaelis-Menton equation that describes the rate of a single enzymatic reaction as a function of a substrate concentration. Photosynthesis is not a true Michaelis-Menton case because it is an integration of photochemistry and a chain of enzymatic reactions. The reductionist might argue that we should model photosynthesis as a function of the photochemical and the enzymatic reaction rates. Further, it is obvious that temperature, substrate availability, and several other factors are important in photosynthesis. Also, since equation 4 considers only light and (indirectly) CO_2 effects, it falls short of our first criterion, that the model be a system model insofar as possible. These points bring up our third criterion: resolution level.

Resolution

According to Klir (1969) every quantity we observe must be determined in space. That is, CO_2 concentration, incident radiant energy, and temperature may be specified at some point in space. This specification may be irrelevant for some studies (e.g., the location of a laboratory may be trivial with respect to the study) but when concerned with a weather forecast, it would be important to identify the spot on earth where temperature is measured. We may also specify the interval and accuracy of our measurements, giving the *space-time resolution level* (Klir 1969).

It may be convenient to think of the spatial resolution level as the *hierarchical level* of

resolution (von Bertalanffy 1969). Biological systems can be placed in hierarchies corresponding with levels of organization (table 1).

Table 1.—Levels of organization

0. $? \rightarrow \infty$	7. Organism
1. Subatomic	8. Community
2. Atomic	9. Global
3. Molecular	10. Solar System
4. Subcellular	11. Galactic
5. Cellular	12. Universe
6. Organ or tissue	13. $? \rightarrow \infty$

Thus a system can be thought of as a component in a larger system, and composed of subsystems (von Bertalanffy 1969). Each level of organization seems to have certain properties unique to that level, making prediction of system behavior from the viewpoint of the lower systems somewhat hazardous. This concept is implicit in the idea of nonsummativity of systems. The reductionist might argue against this view, but the limits of reductionism are obvious. It is impossible to predict all the behavior of a tree from the molecular level. If we hope to discover general ecosystem principles comparable to the fundamental principles of physics, probably we will have to emphasize study from the ecosystem level. The ideal gas law, for example, was derived from observations of the behavior of 10^{23} particles acting in concert. In ecosystem study, we are among the particles; a holistic view is needed.

There are three levels of resolution under consideration for the photosynthesis model: the leaf, tree, and stand levels. Each level will require a different model and approach; we cannot extrapolate the leaf level model to a tree by multiplying the results by the number of leaves in the crown. The temporal resolution of the models will be somewhat flexible at the leaf level, but will probably be on a daily basis for the stand model.

Practical Considerations

There are several practical considerations

which may be of importance in model selection or approach. Some nonlinear systems of differential equations are extremely difficult to solve and their solution may consume a great deal of computer time. Parameter estimation is often a significant problem in many models. Some models require highly precise measurement of input variables, reducing their practical applications, but their theoretical contributions may be important. On the other hand, we sometimes settle for use of a linear regression model when the system is poorly understood and it is much easier to measure the variables than to determine their exact interrelations. Such models are useful in science, but have some built-in dangers, e.g., the hazard of extrapolation of linear regression models.

One danger of reliance upon regression models is that the confidence in the model is greatest at the mean and diminishes at the extremes. In fact, it is possible to fit a curvilinear function to data of a given range, only to have the model become totally inadequate at the extremes.

For example, net photosynthesis as a function of temperature can be described as a symmetrical quadratic (Pisek and Winkler 1958, Webb 1972) (fig. 3).

$$Pn = \beta_0 + \beta_1 T - \beta_2 T^2 \quad (6)$$

But extrapolation of the curve in either direction will lead to progressively more negative

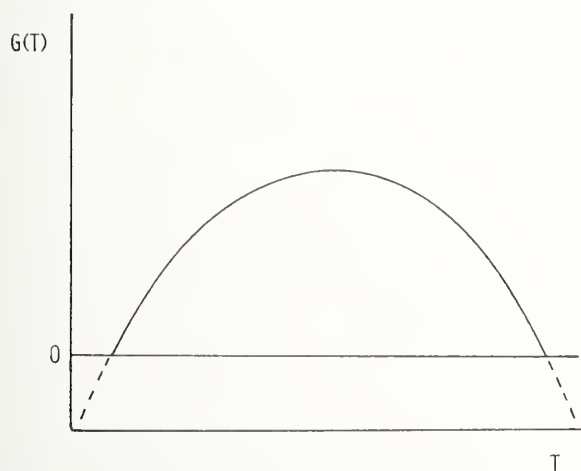


Figure 3. Net photosynthesis, $G(T)$, as a quadratic function of temperature.

values. Thus equation 6 is valid only in the range of temperature within which the parameters were estimated.

The failure of a model to predict system behavior at extremes is not necessarily fatal; such models are common in physics, e.g., the ideal gas law and Newtonian physics. It is necessary to understand the limitations of one's models to know when the system deviates from the model.

In choosing a model, it is important to understand the assumptions and limitations of the model. For example, it is questionable to describe a biological system with a model that assumes a closed reversible system. The assumptions implicit in the model should be compatible with present knowledge of the system of interest.

This is not to say that models of different systems cannot be used to model another system. The idea of isomorphism of systems models is central to general systems theory (von Bertalanffy 1969). Thus thermodynamic models, for example, may be of great utility in certain biological systems models. It remains for the researcher to be sure that the systems are isomorphic so that such models are applicable.

Examination of Some Models of Photosynthesis

The discussion above dealt with criteria for selection of models. It would be useful to discuss some models described in the literature.

Leaf Environment Model

Botkin (1969) simulated photosynthesis in an open oak-pine forest near Brookhaven National Laboratory. He developed a linear model of net photosynthesis:

$$Pn = \beta_0 + \beta_1 T + \beta_2 \ln S + \beta_3 (\ln S)^2 + \beta_4 T^2 + \beta_5 T \ln S \quad (7)$$

where T = leaf temperature, $^{\circ}\text{K}$

S = solar radiation, $\text{gcal cm}^{-2} \text{ min}^{-1}$

Pn = net photosynthesis rate,
 $\text{mg CO}_2 (\text{g dry wt})^{-1} \text{ hr}^{-1}$

β_i = parameters to be estimated

Equation 7 was derived from equation 8 and equation 9:

$$P(L) = a + b \ln S \quad (8)$$

which had been used to fit photosynthesis data from several herbaceous species (Blackman and Rutter 1946, Blackman and Wilson 1951). Equation 8 was coupled with equation 9 suggested by data of Pisek and Winkler (1958), Krueger and Ferrell (1965), and others:

$$G(T) = a + bT + cT^2 \quad (9)$$

Data from two species of oak were obtained from infrared gas analysis and were used to estimate the parameters of equation 7 by stepwise multiple regression analysis. Some of the terms of equation 7 were nonsignificant, and were thus discarded. The final model was:

$$Pn = \beta_0 + \beta_1 T + \beta_2 \ln S + \beta_3 T \ln S \quad (10)$$

Having estimated the parameters of equation 10, the model was used to predict photosynthesis of oak in the field. Their model gave fair to good agreement with subsequently measured net photosynthesis.

In terms of the criteria discussed above, equation 10 is generally inadequate. It does allow for interaction between two variables but fails to take into consideration other factors that affect photosynthetic rate (stomatal behavior, micrometeorological conditions, plant nutrition). The model does satisfy the requirement that the Pn model be *solved* as a function of systems variables, that is, $Pn = f[S, T]$.

In terms of the other criteria, the model falls short of having a great deal of theoretical validity in that the function is one of convenience rather than having general physical-chemical meaning. It is unnecessary to discuss in detail Botkin's model with respect to the other criteria. Like most photosynthesis models, it is specified at the leaf level, where the inputs to the leaf are measured, and the

relations between the leaf subsystems are inferred.

While his model has many failings, it does have one virtue. If one were interested in comparing $Pn = f[T, L]$ in two species under identical conditions, this model may be adequate, given that some other factor, e.g., stomatal resistance, is not limiting. The fact that the parameters of the model were estimated by least-squares allows the use of statistical tests useful in comparing such data.

Energy Budget Model

Idso and Baker (1968) based their model of photosynthesis and their earlier model (Idso and Baker 1967) on that of Gates (1965) which is an energy budget model where precise measurement of incoming radiant energy is equated with outgoing energy. Thus, at equilibrium, the amount of energy leaving a leaf is equal to that coming in. Gates' (1965) leaf energy budget model is:

$$a_s \frac{(1+r)(S+s)}{2} + a_t \frac{(R_g + R_a)}{2} - \epsilon_t \sigma T_l^4 \pm C \pm LE = 0 \quad (11)$$

where a_s = mean total absorbance of plant to sunlight and skylight

r = reflectance of underlying ground or plane surface to sunlight and skylight, S and s

a_t = absorbance of plant to thermal radiation, R_g and R_a

ϵ_t = emissivity of plant to thermal radiation

T_l = leaf temperature $^{\circ}\text{K}$

C = energy gained or lost by convection $\text{cal cm}^{-2} \text{ min}^{-1}$

L = latent heat of evaporation $\text{cal cm}^{-2} \text{ min}^{-1}$

E = transpiration rate of leaf $\text{gm cal}^{-2} \text{ min}^{-1}$

S, s, R_g, R_a = various short and long wave radiation inputs $\text{cal cm}^{-2} \text{ min}^{-1}$

The first three terms of equation 11 represent the radiant energy available to the plant. By elaborating equation 11 and solving for T_l , Gates was able to predict leaf temperature as a function of the incoming energy less the outgoing energy. From data of other workers he developed a family of curves for photosynthesis with respect to temperature and radiant energy. Given these curves and by calculating T_l , Gates predicted photosynthesis of several species.

Idso and Baker (1967) constructed a similar family of curves for sorghum. In a subsequent paper (Idso and Baker 1968), they used these curves to predict P_n on four different types of days based on input from their energy budget calculations. They did not measure P_n directly, so there was no direct verification of the models.

In terms of our suggested criteria for analysis of models, it is obvious that the energy budget model is consistent with the systems approach. However, the relation of T_l and absorbed energy to P_n is empirical and incomplete, and constitutes the weak point of this model. Thus, from a standpoint of theoretical validity, the P_n model suggested by Idso and Baker (1967, 1968) suffers from drawbacks identical to those of Botkin (1969). Should a more satisfactory model of P_n as a function of light and temperature become available, however, it can be incorporated into the leaf energy budget model. The energy budget model itself is sound and has great promise. It is probably sufficiently general to apply to any plant, and the various terms can be refined where more specific component models are needed.

Unfortunately, from a practical standpoint, the input data necessary for such a model are very difficult to obtain, requiring a great deal of sensitive instrumentation. This limitation would preclude the applicability of the model to study of some ecosystems where such measurements would be most difficult or impossible. Further, the resolution of the model is great, and such variables as incident solar angle and leaf geometry are important. Extrapolation of this model to a tree or to a stand would require prodigious volumes of input data and highly sophisticated subsystem

models.

In summary, the high-resolution energy budget approach, while having considerable appeal from the systems and theoretical standpoint, is probably limited in its utility to theoretical studies and studies of simpler systems. The basic approach could be modified by altering the resolution level of the components and by perhaps adding some stochastic models. In this way, the energy budget approach could be used in modeling at a lower level of resolution. Such a model, being simpler, could then be used at the tree and stand levels of organization.

While the work of Gates (1965) and his colleagues has contributed greatly to the understanding of the energetics of the leaf, it still remained to develop a model of the process of photosynthesis itself that could satisfy our second criterion, that of theoretical validity. This problem was attacked by Brown (1969).

Process Models

Brown assumed that if P_n is a first-order reaction, then equation 12 would hold:

$$P = KI[CO_2]g \quad (12)$$

where P = rate of CO_2 exchange per unit leaf area

K = capacity of acceptor site in the leaf to fix CO_2 at the site of photosynthesis

I = incident radiation

$[CO_2]g$ = concentration of CO_2 at the fixation site

Brown also assumed that I follows Beer's law within the leaf,

$$I_x = Ie^{-ax} \quad (13)$$

where I is incident radiation at the leaf surface, a is the extinction coefficient, x is distance from the leaf surface, and I_x is radiation at x . Brown incorporated equation 12 into Gaastra's (1959) derivation from Fick's law of diffusion representing steady-state diffusion of CO_2 from the air to the leaf:

$$P = \frac{C_a - C_c}{\Sigma r} \quad (14)$$

where C_a = concentration of atmospheric CO_2 g cm^{-3}

C_c = concentration of CO_2 at the chloroplast g cm^{-3}

Σr = resistance to gas diffusion sec cm^{-1}

giving

$$P = \frac{D[\text{CO}_2]a}{1 + D/KI} \quad (15)$$

where D is the integral exchange coefficient

$$D = \frac{1}{r_a + r_s + r_m} = \frac{1}{\Sigma r}$$

where r_a is boundary layer resistance, r_s is stomatal resistance, and r_m is mesophyll resistance to CO_2 diffusion in sec cm^{-2} . Equation 15 is gross photosynthesis, not P_n , and thus equation 15 should be corrected for respiration:

$$P_n = \frac{K[\text{CO}_2]aI - R}{1 + KI/D} \quad (16)$$

where R is respiration.

These models assume that resistance to transfer of CO_2 from respiration site to the photosynthesis site is negligible. The variable nature of r_s must also be considered, requiring an additional model of stomatal behavior. Brown (1969) notes that the complexity of equation 16 becomes great when other components are added, and states that it is necessary to solve equation 16 by arriving at the functional relationships of the components by independent means and substituting them into the general model.

If the components are truly independent, such a tactic is valid. If not, error is introduced by failing to consider changes in the values of the parameters due to interaction, a violation of our systems criterion.

Lommen and coworkers (1971) took an approach similar to that of Brown (1969). They began with Gaastra's (1959) derivation from Fick's law of diffusion now familiar to us. The biochemical relations are described by a Michaelis-Menton type equation that describes the rate of a single enzymatic reaction. Their model for photosynthesis as a function

of chloroplast concentration of CO_2 is:

$$P = \frac{P_m}{1 + K/C_c} \quad (17)$$

where P = photosynthesis $\text{g cm}^{-2} \text{sec}^{-1}$

P_m = photosynthesis at saturating CO_2 $\text{g cm}^{-2} \text{sec}^{-1}$

K = concentration of CO_2 at the chloroplast when $P = \frac{1}{2}P_m$

C_c = concentration of CO_2 at the chloroplast g cm^{-3}

Equation 14 is solved for C_c and substituted into equation 17 giving photosynthesis as a function of atmospheric CO_2 concentration and stomatal resistance:

$$P = \frac{(C_a + K + \Sigma r P_m)}{2 \Sigma r} - \frac{[(C_a + K + \Sigma r P_m)^2 - 4 C_a \Sigma r P_m]^{1/2}}{2 \Sigma r} \quad (18)$$

They also derived a similar though more complex model giving photosynthesis as a function of C_a , K , P_m , W , and two series of resistances, S_1 , S_2 ; W is respiration.

They also derived submodels of photosynthesis as a function of light and temperature,

$$P_m(L, T) = \frac{P_m L T G(T)}{1 + K_L/L} \quad (19)$$

similar to equation 4 but incorporating a term $G(T)$ representing the temperature dependence of photosynthesis. The authors implied that equation 19 could be incorporated into equation 18 and their other model, but they did not do so, and dimensional analysis of equation 18 with $P_m L T$ and K_L substituted for P_m and K , shows that such a substitution is physically unrealistic. Hence the model of Lommen et al. (1971) is inadequate for predicting photosynthesis as a function of light and temperature as well as CO_2 concentration and stomatal resistance.

Chartier (1966, 1969, 1970) also developed a complex model of net assimilation derived along the lines of that by Lommen et al. (1971). Beginning with the fundamental form (Chartier 1970):

$$P = F + R$$

where F = net assimilation rate
per unit leaf area

R = respiration rate

and by analogy to Gaastra's (1959) Fick's law function, he derived:

$$F + R = \frac{C - F(r_a + r_s + r_m) - nRr_m}{\frac{1}{aE} C - F(r_a + r_s + r_m) - nRr_m + r_x} \quad (20)$$

The only terms unfamiliar to us are r_x , n , aE , and R . Here R is respiration in light, and n is the fraction of respiratory flux that is mixed in the intercellular spaces ($n \leq 1$). The term aE represents conversion of light to photosynthate where E is incident light energy, and a is the efficiency of light energy conversion. The term r_x represents resistance to carboxylation, a parameter which includes biochemical restraints caused by mineral nutrition, age of the leaf, etc.

Chartier's (1970) model differs from that of Lommen et al. (1971) in that the effect of light is incorporated into the model. The effect of temperature must be included, perhaps by a multiplicative term (Lommen et al. 1971, Webb 1972). Chartier's model gives a quadratic solution for F , as in Lommen et al, but many of the terms in both models are difficult if not impossible to measure in a field study. Further, respiration is represented by a single term; an oversimplification requiring further work.

Conclusions

In order to be consistent with the systems viewpoint, photosynthesis must be treated as a *Gestalt*, or nonsummative system. The models described above violate this criterion to some extent, most often by failing to incorporate an important factor in the model. We had hoped to be able to use one of the models by Lommen et al. (1971) or by Chartier (1970) as a tool in our field research, but two considerations prohibit this: (1) both models have unmeasurable (in the field) terms, (2) neither model is complete, i.e., neither expresses photosynthesis as a function of *all* the known important factors.

Consequently, it will be necessary to develop a model of photosynthesis as a function of light, temperature, leaf resistance and ambient CO_2 concentration with some simplifications from the above models which will increase the utility of the models. The parameters in this model will be estimated from data after the manner of Webb (1972) by nonlinear least-squares. The final model will have much the same utility as a regression model, but will not be linear and the parameters where possible will have physical meaning. Thus, the models will be developed with certain specific goals in mind, necessitating development of different models for the tree and stand levels of resolution.

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A model of light and temperature controlled net photosynthetic rates for terrestrial plants

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Abstract

Steady-state relative net CO₂ exchange was modeled in terms of a temperature-dependent respiration function and light- and temperature-dependent photosynthesis function. The parameters of the model were evaluated using the laboratory CO₂ exchange data of a group of 40 red alder seedlings (Alnus rubra Bong.). The model is continuous and well-behaved in the temperature region of 0-50°C for light energy between 0.0 and 1.0 ly/min total short-wave radiation.

Introduction

Consumer populations depend upon the chemical energy that is converted from solar energy by plants in the ecosystem. The rate of conversion, or net photosynthesis, is in turn dependent upon the genetic information available to each plant and its immediate environment. Many factors influence net photosynthesis but, as Schulze (1970) found from his work in a beech stand, when water stress is not appreciable, the radiation and temperature regimes of the plant largely regulate net photosynthesis. This paper presents an empirical model of steady-state net CO₂ exchange in terms of a light (L) and temperature (T) controlled gross photosynthesis function (Ps) and a temperature-controlled dark respiration (Rs) function.

Net CO₂ flux entering the leaf, or net photosynthesis (Psn), is conceptualized as the difference between carbon fixed in the photosynthetic process and that lost during respiration, $P_{sn} = P_s - R_s$ (Larcher 1969). The two

terms, net photosynthesis and net CO₂ exchange, are used synonymously in this paper. Although the former is less general in that it usually applies only to CO₂ exchanges occurring in the light, it is more mechanically viable.

Fluxes of CO₂ are easily measured and many investigators have reported on the net photosynthetic response of plants to temperature and light (Heath 1969, Rabinowitch 1969, Milner and Hiesey 1969). Figure 1 illustrates the net photosynthetic response of small plants or individual leaves to increasing temperature or light. The linear portion of the light curve represents the rate of the photochemical reaction at the chloroplast and is largely invariant among species (Rabinowitch 1969). This linear slope can be extrapolated through zero CO₂ flux, called the light compensation point, and the negative abscissa intercept interpreted as dark respiration (Chartier 1969). At high light levels, photosynthesis becomes saturated and its rate is dependent upon factors such as temperature

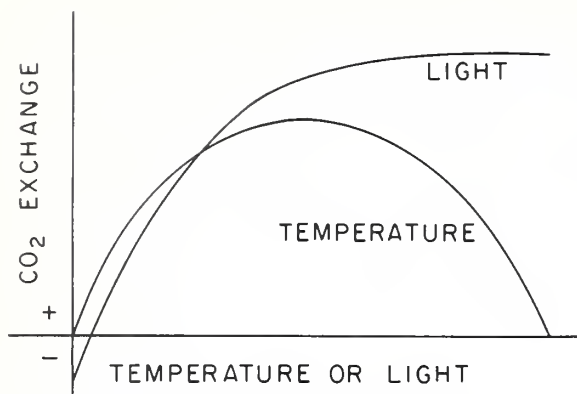


Figure 1. Leaf CO₂ exchange as related to light and temperature.

and water potential that influence the carbon-fixing enzymatic reactions.

Net photosynthetic response to temperature, also shown in figure 1, is generally a symmetrical form (Pisek et al. 1969, Mooney and Harrison 1969). Pisek's data have shown that the slope of the curve and the point of maximum shifts depending upon species and season but the response remains symmetrical.

The responses to light and temperature seem well-defined. A model using light and temperature as independent variables should conserve the known responses to each as well as include any interaction. To be useful, the model should also predict CO₂ losses that occur below the light-compensation point as well as respiration losses occurring during darkness. This requires that a respiration response be explicitly introduced into the model.

Figure 2 represents a generalized dark respiration response to temperature for steady-state conditions. The response at low and intermediate temperatures is exponential in keeping with the van't Hoff Q_{10} rule for chemical reactions (Forward 1960). Above some high temperature, a decline resulting from enzyme denaturation occurs which tends to become irreversible as the time of exposure to high temperature increases (Forward 1960, Longridge 1963).

Net CO₂ uptake, or net photosynthesis, can now be expressed in terms of temperature-controlled respiration and light- and temperature-controlled photosynthesis. For

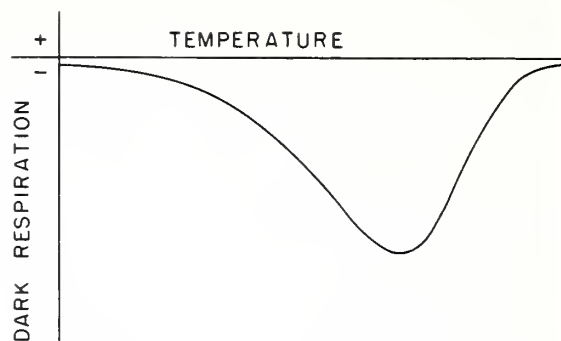


Figure 2. Effect of temperature on dark respiration.

purposes of this model, net CO₂ fluxes into the leaf are assigned a positive value while CO₂ losses are considered negative.

$$P_{sn}(L,T) = P_s(L,T) - R_s(T) \quad (1)$$

The functional form of the model can be expanded around the following exponential expression that is representative of the light curve in figure 1.

$$P_{sn}(L,T) = B_0(T) (1 - \exp(B_1 L)) - R_s(T) \quad (2)$$

$R_s(T)$ is negative and represents dark respiration. $B_0(T)$ represents the light-saturated asymptote as a function of temperature. The exponential coefficient (B_1) determines response behavior at low light levels and is characteristically independent of temperature. $B_0(T)$ can be represented by a quadratic function of the following form:

$$B_0(T) = B'_0 + B'_1(T - B'_2)^2 \quad (3)$$

Where:

B'_0 : maximum photosynthesis
 B'_1 : slope coefficient; negative algebraic sign
 B'_2 : temperature of maximum photosynthesis

Respiration as a function of temperature ($R_s(T)$) can be modeled with the following expression:

$R_s(T) = B''_0 \exp(B''_1(T - B''_2)) - \exp(B''_1(T - B''_2))$
 $B''_0/\exp(1)$: maximum respiration
 B''_1 : slope coefficient; positive sign
 B''_2 : temperature of maximum respiration

This function is asymptotic to zero respiration at both low and high temperatures and exhibits an exponential increase in respiration followed by a rapid decline at high temperatures.

The completed functional expression for $P_{sn}(L,T)$ is:

$$P_{sn}(L,T) = -B_0 \exp[B_1(T-B_2) - \exp(B_1(T-B_2))] + [B_2 + B_3(T-B_4)^2] [1 - \exp(B_5 L)] \quad (4)$$

The intent of this model is to predict net photosynthesis in light and CO_2 losses in darkness. The model is not useful for predicting gross photosynthesis without including some function for respiration in the light. Until the experimental techniques for obtaining such measurements are developed, the light respiration term must remain implicit in the gross photosynthesis function. This limits the use of the model although most C_3 plants will respond similarly. A different model may be required for C_4 plants such as grasses that require a much higher light level to saturate photosynthesis.

Methods and Materials

Values for the six parameters in the model were determined with a least squares fit of the data using an algorithm developed by Marquardt (1963). Net photosynthetic data were taken with a controlled environment system developed by Webb (1971). The test organism for the model was red alder (*Alnus rubra* Bong.).

Forty red alder seedlings, 1- to 2-years-old, were removed from the field and propagated in a nutrient culture before transferring them to the gas-tight controlled environment chamber. The root system of the seedlings was enclosed in a nutrient flow system with temperature controlled at $11^\circ C \pm 1^\circ C$. The plants were maintained in this system for 1 month at conditions of light and temperature consistent with those in the greenhouse.

Carbon dioxide absorption rates were meas-

ured by monitoring the CO_2 depletion in the gas-tight environment chamber with a Beckman IR gas analyzer. Atmospheric CO_2 levels in the chamber were maintained between 320 and 335 p.p.m. Light energy was varied from 0.06 to 0.68 ly/min (total shortwave radiation) at air temperatures from 5 to $30^\circ C$. For each of five light levels, CO_2 uptake was measured while temperature was changed at the rate of 1° per 5 minutes beginning at $15^\circ C$ and proceeding upscale to approximately $30^\circ C$. Measurements were then made while decreasing temperature at the same rate until near $5^\circ C$ at which time temperature was increased again up to $16^\circ C$. All CO_2 uptake measurements were made during 3 successive days. Relative humidity varied between 65 percent at low temperatures to 75 percent at high temperatures.

Results

A portion of the data is plotted in figures 3 and 4. The photosynthetic response to radiation in figure 3 is characterized by a linear response at low light followed by the usual light-saturated response at high radiation. This is consistent with the findings of many other investigators. The saturation value for net photosynthesis increases with temperature, but the increase is not linear.

Figure 4 shows the net photosynthetic response to temperature for constant radiation of 0.19 ly/min. A quadratic function was fit to the data and the parameters with their respective standard errors are listed in figure 4. At 0.19 ly/min, net photosynthesis has a maximum of $20.5^\circ C$. Although these data represent the temperature range between 5.5° and 27° , the data of Pisek et al. (1969) indicate a nearly symmetrical response between 5° and $40^\circ C$. Extrapolation of the quadratic beyond this temperature range should be done cautiously although Phillips and McWilliams (1971) have measured zero CO_2 fluxes at high temperatures. It may be that high temperatures increase respiration until it exceeds the photosynthetic capacity.

Figure 5 illustrates the response surface generated by expression (4) which is the net

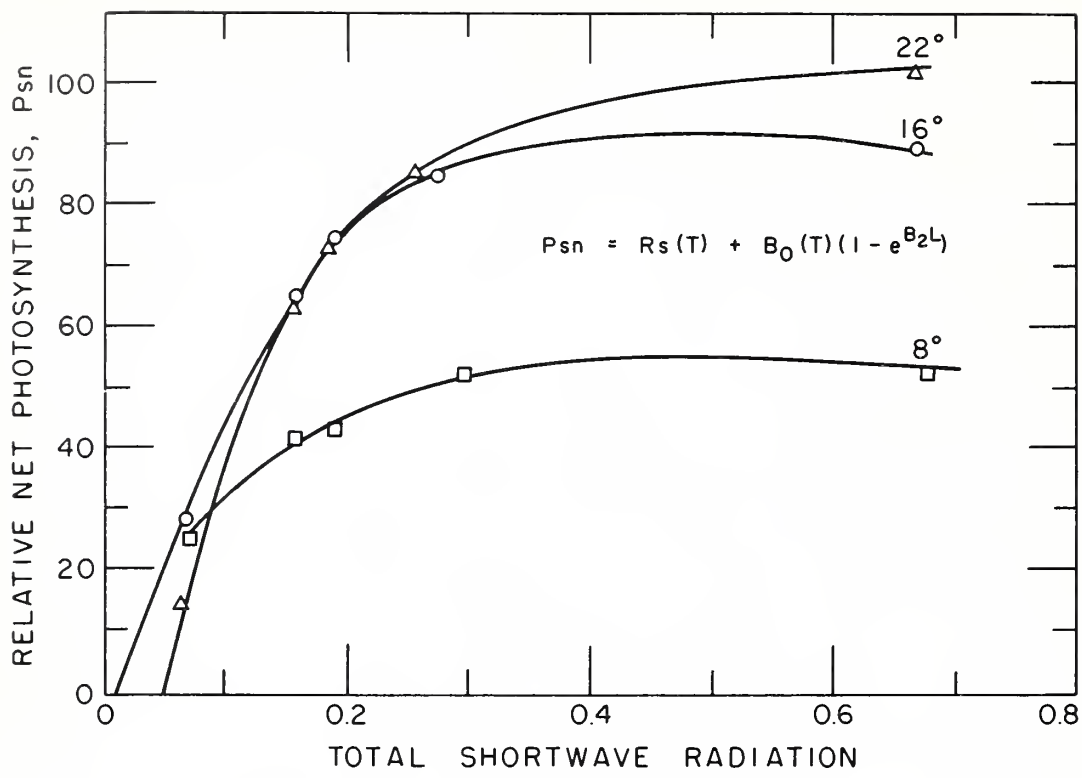


Figure 3. Light effects on net photosynthesis of red alder at three temperatures.

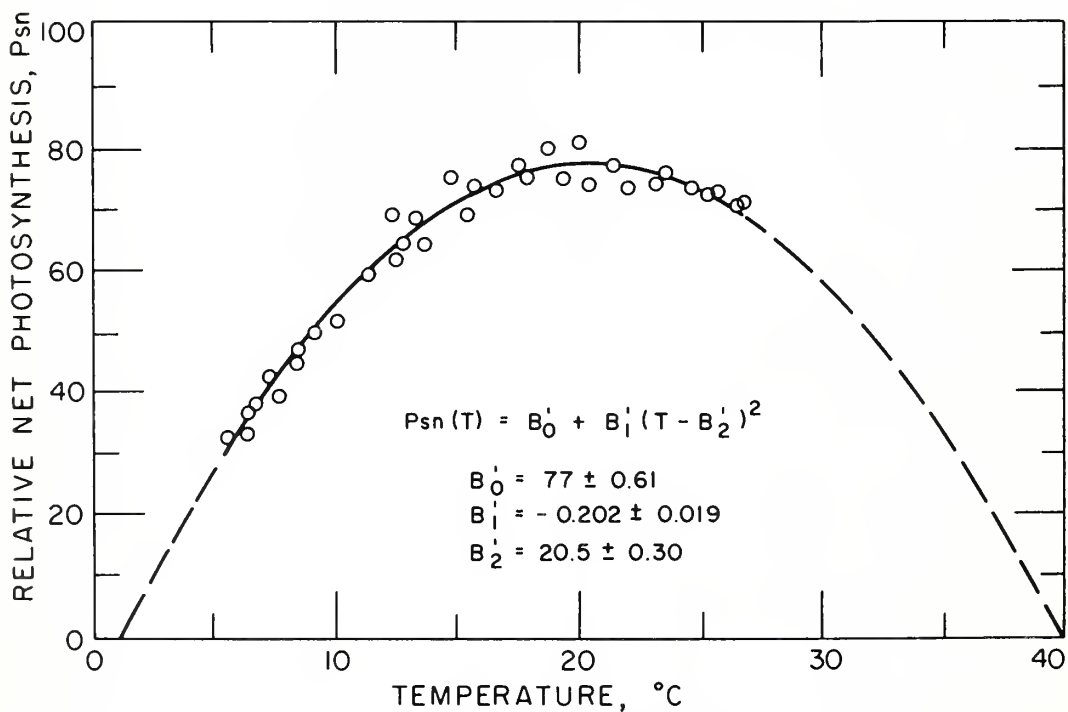


Figure 4. Net photosynthetic response of red alder to temperature at 0.19 ly/min total s.w. radiation.

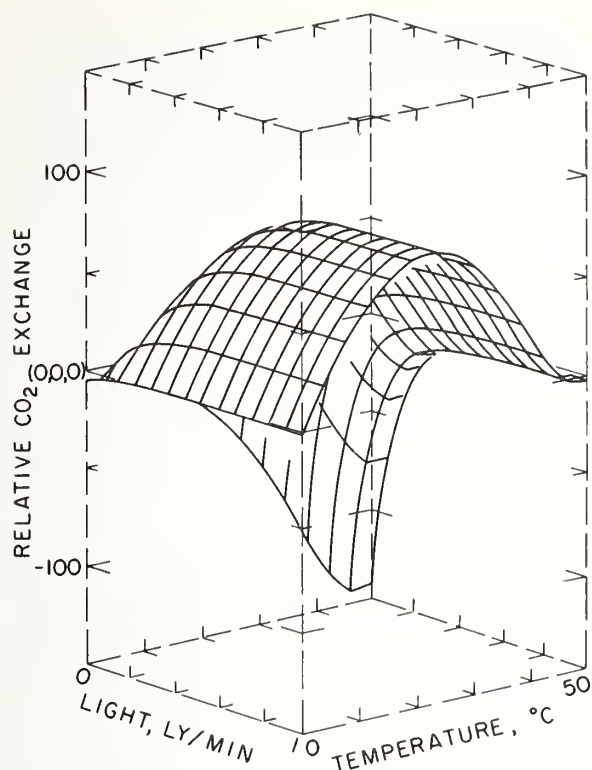


Figure 5. Response surface of net CO_2 exchange generated by $\text{Psn}(L,T) = -513.3 \exp[.088(T-47.7)] - \exp .088(T-47.7)] + [187.3 - .105(T-41.4)^2] [1 - \exp(-9.59L)]$.

photosynthetic response to both light and temperature. The functional form of the surface is included in figure 5 along with the values of the 6 parameters obtained from a least-squares fit of the CO_2 exchange data. The average deviation of the function from the data was ± 9.1 -pct. and the r^2 was 0.97.

Note that the light saturation phenomenon of photosynthesis is conserved in this model as well as the symmetrical response to temperature. Although there are no data below 5° and above 30° , the model seems well-behaved in the regions outside the data. As light decreases the gross photosynthesis function tends toward 0, and the dark respiration function begins to dominate. Below the light compensation point CO_2 fluxes become negative. At zero light only respiration occurs, and because the function goes asymptotically to zero at both low and high temperatures, the model never predicts an uptake of CO_2 in darkness.

The important interaction between light and temperature can best be shown by numerical example. Table 1 shows the predicted temperature of maximum net photosynthesis, or optimum temperature, and the peaks of net photosynthesis for each of five levels of light. Both the optimum temperature and the peaks of net photosynthesis increase with light. The latter is exemplary of photosynthetic light saturation.

Table 1.—Predicted effect of light on maximum net photosynthesis

Light ly/min	Relative maximum Psn	Temperature of maximum Psn
0.07	27.8	16
.15	65.5	20
.19	76.2	21
.25	90.8	22
.68	100.0	23

The increased temperature of maximum net photosynthesis associated with additional light can be explained as an interaction between the gross photosynthesis function and dark respiration. At low light, photorespiration is minimal and photosynthesis is largely independent of the temperature increases that step-up dark respiration. Therefore, dark respiratory CO_2 losses from cellular maintenance are not compensated by photosynthesis as temperatures rise and maximum net photosynthesis (photosynthesis minus respiration) occurs at a relatively low temperature. As light increases, photosynthesis and its dependence on temperature increases. This allows photosynthesis to keep pace with temperature-controlled dark respiration and maximum net photosynthesis then shifts to a higher temperature.

Although the model is empirical, it has several noteworthy features. The model is continuous over a wide range of independent variables and is therefore more mathemati-

cally tractable than discontinuous or piecewise continuous models. This continuous feature should facilitate linking this model to others.

The general net photosynthetic response of plants to light and to temperature has been demonstrated with many different species under various preconditioning treatments. The general responses characterized in figure 1 predominate with various shifts in the peak and magnitude of the response curves. These shifts can be described mathematically by determining CO_2 exchange at certain points and using these data to define parameters in the basic model.

In the Biome program, CO_2 exchange studies are being conducted on several species and these data will further test the model proposed here. A necessary addition to the model is an explicit evaluation of light respiration from which techniques for data acquisition are now being contemplated.

Acknowledgments

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Energy flux studies in a coniferous forest ecosystem

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Abstract

The fluxes of thermal energy between the atmosphere and a young Douglas-fir forest were measured during two contrasting summer days, one cloudless and one overcast. The energy budget components were evaluated by the Bowen ratio method, with ceramic-wick psychrometers at the 26.16 m, 28.16 m, or 31.16 m levels. The maximum height of the tallest trees was 28 m, and the general level at the top of the closed canopy was about 22 m. Daily totals of the energy budget components (cal/cm^2) under cloudless skies on July 29, 1971, were: solar radiation, 584; net radiation, 410; change in storage, 5; convection, -135; and latent energy, -280. The albedo was 0.09 on both the clear and the overcast day. Analysis of the overcast conditions of July 31, 1971, yielded the following values: solar radiation, 171; net radiation, 134; change in storage, 6; convection, -39; and latent energy, -102.

Problems of measurement and analysis are discussed. These include the storage term in the biomass, and the small gradients of potential temperature and vapor pressure above the canopy. Clear day gradients at noon, for example, were in the order of $-0.03^\circ\text{C m}^{-1}$ and -0.03 mb m^{-1} . Techniques are presented for minimizing measurement errors.

Introduction

The level of biological activity at the surface of the earth is closely associated with cycles of energy and mass. The cycles of mass and of energy are virtually interchangeable concepts. Indeed, the transpiration and photosynthetic components of the mass cycle can be studied through examination of the cycle of energy, with the energy required to change the phase of H_2O and CO_2 serving as the connecting link.

The magnitudes and phase relationships of the mass and energy cycles are affected by the characteristics of the surface, and by the state of the atmosphere. The properties of vegetation, particularly of low, cultivated ecosystems, have been investigated thoroughly in a variety of studies that have clearly demonstrated many advantages for energy budget evaluations of transpiration and photosyn-

thesis (Baumgartner 1965). The advantages include sensitivity, mobility, and the benefits to be gained by use of a nondestructive technique. The application of these techniques to the forest ecosystem appears feasible and useful. A number of studies have already been reported, but in general the effects of forests upon the cycles are not yet well known (Baumgartner 1971, Tajchman 1971). Coniferous forests, as a class, are good absorbers of solar radiation. The roughness of coniferous crowns also appears to effectively enhance mixing in the atmosphere near the top of the canopy. These factors, combined with the large surface area of canopies, make forests into very efficient exchange surfaces for water vapor, carbon dioxide, and energy.

Studies of the fundamental cycles of energy and mass have begun at the Cedar River site in the Coniferous Forest Biome. A variety of interrelated studies are planned in coopera-

tion with physiologists, soil scientists, hydrologists, and meteorologists. The work reported here is of preliminary research into the exchange of thermal energy between a young Douglas-fir forest and the atmosphere. The energy exchange processes have been evaluated during two contrasting conditions: the first during clear, warm weather characterized by a large energy input to the forest, and the second during cool, overcast conditions with a relatively small energy input to the forest. The objectives are to define the energy transfer characteristics of the young forest under conditions of both high and low rates of transpiration. Study of these contrasting conditions will help us to understand the processes that control the exchange of energy and water vapor between the forest canopy and the atmosphere.

Experimental Methods

The evaluation of thermal energy exchange in the forest is simple in concept, requiring that appropriate boundaries be defined about the forest site, that the quantities of energy crossing the boundaries be identified, and that appropriate measurements be made at periodic intervals. The periodic samples can then be combined to yield estimates of energy exchange for the desired time interval. The selection of an appropriate model is an important step in evaluating the thermal energy exchange.

Energy Transfer Models

Several review articles have discussed the application of various energy transfer models to the problem of evaluating the exchange between the forest and the atmosphere (Baumgartner 1965, Federer 1970, Fritschen 1970).

The basic problem concerns the transformation of energy by the forest from radiant to nonradiant forms. The total energy thus transformed is called net radiation, Q^* ; this equals the quantity of radiation of all wavelengths absorbed at the surface, minus the radiation lost by reflection and emission. The

net radiation is transformed into either a change in stored heat in the soil and biomass, G ; a flow of convective (sensible) energy between the forest and the air, H ; or a flow of latent heat, λE , that is associated with a flux of water vapor E . The amount of energy transformed in photosynthesis, P , is of great importance in productivity. However, since it amounts to only a few percent in terms of the net radiation flux over the forest (Denmead 1969), P will be neglected in this study.

The rate and direction of energy transfer depends upon the relative energy states of the canopy and the atmosphere and upon the availability of radiant energy which is derived primarily from the sun. The state of energy is determined by temperature and by vapor concentrations. Motion of the atmosphere may also enhance energy transfer. Energy transfer models thus use measurements of temperature, vapor concentration, wind, and radiant energy in order to determine the flow of energy between the forest and the atmosphere.

The "Bowen ratio" model was selected for use in this study because of relative simplicity in analysis and application, and because of its general acceptance based upon tests over other types of vegetation. The method was first derived by Bowen (1926), and has been adapted for energy transfer studies by a number of workers (Fritschen 1965, Tanner 1960).

The Bowen ratio model has been thoroughly described elsewhere, but a short discussion here will help to place its application into perspective. First, we must sum the thermal energy fluxes active in the forest in accordance with the principle of conservation of energy, to obtain

$$Q^* + G + H + \lambda E + P = 0. \quad (1)$$

The polarity convention considers fluxes to the surface as positive. After neglecting photosynthesis, equation 1 can be solved for latent energy to yield

$$\lambda E = -(Q^* + G) / (1 + \beta) \quad (2)$$

where β is the Bowen ratio of convective heat to latent heat ($H/\lambda E$). The Bowen ratio can be written

$$\beta = H / \lambda E = \gamma \Delta\theta / \Delta e \quad (3)$$

where γ is the psychrometric constant ($\gamma \approx 0.66$ mb/ $^{\circ}$ C at sea level) and $\Delta\theta$ and Δe represent the measured differences in potential temperature and in vapor pressure at two levels in the atmosphere above, but near, the surface.

The Bowen ratio model thus provides a rationale for partitioning the measured supply of thermal energy into convection and latent heat, based upon measurements of temperature and vapor concentration at only two levels above the canopy surface. Wind measurements are not required for the analysis, although they are often useful in interpretation of the results. The supply of thermal energy ($Q^* + G$) is measured, so limits are placed on the estimates of convection and latent heat with this method.

The disadvantages of the model are primarily associated with instrumentation; accurate measurements are required in order to measure the small gradients in temperature and vapor found near the forest canopy. In addition, the basic relationship in equation 2 becomes undefined whenever $\beta = -1$. This normally occurs infrequently, and ordinarily only for short periods near dawn or dusk when the amount of available energy is limited. The magnitude of H and λE will normally be small at such times.

Site Conditions

The energy exchange studies were carried out in the broad, flat valley of the Cedar River, near Seattle, Washington. The soil and stand conditions have been described by Fritschen (1972). The stand is second-growth Douglas-fir approximately 35 years old, with an average of 570 trees per ha. The stand canopy is relatively level; the height of the tips of the tallest trees in the vicinity of the experimental site is about 28 m. The site is adjacent to the lysimeter tree described by Fritschen (1972). A series of energy transfer studies are planned at this site in the future, using the lysimeter tree, meteorological towers, and a variety of models for evaluating energy exchange processes.

Field Measurements

Net radiation, stored heat, and temperature and vapor pressure measurements were obtained with a mobile data acquisition that has been described by Gay.¹ The truck-mounted system includes sensors and supports, cabling, and a digital data logger with resolution of 0.001 percent (0.1 microvolt on a 10 millivolt scale). Ceramic wick, wet-bulb psychrometers of the basic design of Lourence and Pruitt (1969), as modified by Gay (n.d.), were used for the temperature and vapor pressure measurements.

The sensors were mounted on a 33.5 m (110 ft) tall, triangular TV tower about 0.3 m (1 foot) in width. Wind, temperature, and vapor pressure measurements were made at six levels, respectively, 26.16, 27.16, 28.16, 29.16, 30.16, and 31.16 m above the forest floor. The radiation budget components were measured from a height of 30.66 m above the floor. The tip of the tallest tree in the vicinity of the tower extended to 28 m, though the bulk of the crowns were below 24 m, and the general level of crown closure was about 20 to 22 m above the floor. Five soil heat flux disks were installed at the -2 cm level, just beneath the surface of mineral soil on the forest floor.

Observations began on July 27 and continued through August 1. The sensors were sampled at 5-minute intervals during the day, and at 10-minute intervals at night. The observation period spanned a range of weather conditions that included one clear and one completely overcast day. The data acquisition system performed well during this period.

Problems in Forest Energy Budget Analyses

A variety of measurement problems are encountered in energy budget studies. In addition, forests have unique characteristics of scale and mass that affect the application of

¹L. W. Gay. An environmental data acquisition system. National Conference on the Forest, Weather, and Associated Environment, Atlanta, Georgia, May 18-19, 1971. Mimeo., 8 p. Abstracted: Bull. Am. Meteor. Soc. 52: 202-203.

the basic energy budget model given in equation 2. The gradients of temperature and vapor above the rough, porous forest canopy are very slight, and measurement difficulties increase with small gradients. Another major problem is related to the difficulty of measuring changes in stored energy in the biomass of the forest. These problems will be placed into perspective at the Cedar River site, for they affect the analyses and the subsequent interpretation of the results.

Evaluation of Gradients

Gradients of temperature, vapor concentration, and wind are small above forest canopies, even though the transfer of energy and mass may be proceeding at high rates. The small gradients result from mixing induced by the mechanical turbulence created by the rough canopy surface. In addition, the exchange surfaces are distributed through a considerable canopy depth so that the sources of heat and vapor are diffuse, rather than being concentrated as in the dense canopies of crops or other low vegetation. The small gradients above the forest require that extreme care be taken in the development of suitable instrumentation, and in the experimental design controlling the deployment of sensors.

The Bowen ratio model assumed that steady state conditions prevail, i.e., the values of the variables do not change with respect to time during the period of analysis. This is partially satisfied by averaging the values over the period of an hour before applying the model. Integration into hourly means also reduces the small random component of error associated with the measurements. It does not, however, reduce biases that are introduced by small differences among sensors. Such biases can be a source of serious error, particularly with small gradients that exist above the forest. Bias errors must be handled by techniques other than averaging.

Two approaches have been used to cope with the problems involved in the measurement of small gradients above forests. In the first approach, the two levels of measurement required for the Bowen ratio are separated by

a relatively large distance (10 m) in order to increase the differences that are being measured to a level commensurate with the sensitivity of the data system (Galoux et al. 1967, Storr et al. 1970). In the second, reversing sensors have been used to cancel the effect of any small biases that may exist between sensors (Black and McNaughton 1971).

A large vertical separation of the sensors introduces questions of the representativeness of the measured gradients which should represent the effect of the underlying surface. It is quite possible that a sensor placed 10 m above the canopy may be measuring properties of the atmosphere that are derived from a surface other than the one under investigation. In contrast, a pair of reversing sensors, placed near the canopy, offers an excellent means for evaluating small gradients. However, the reversing mechanism introduces new problems of design for operation and support in tall forests.

A graphical approach was used in this study to minimize sensor errors in the gradient measurements used for the Bowen ratio analysis. Initially, the mean hourly values of potential temperature were plotted against the associated values of vapor pressure to yield 24 plots (1 per hour) for each day, with each plot containing six points (one for each measurement level). The plots will be straight lines if similarity exists between the gradients of potential temperature and vapor concentration, providing there are no errors of measurement (Tanner 1963). Since similarity is an assumption of the Bowen ratio method, these plots were used to separate out the instrument levels that exhibited small offsets throughout the day and to identify those levels appropriate for use in the Bowen ratio analysis.

The similarity plots for July 29 are shown for levels 1, 4, 6 in figure 1A, and for levels 1, 2, 3 on July 31 in figure 1B. The potential temperature (θ) scale on the ordinate differs between the 2 days. The vapor pressure (e) scale is shown in the legend. Note that the plot for each hour has been normalized by subtracting the θ and e value at the bottom level from the observations at each of the other levels. Therefore each plot actually shows the incre-

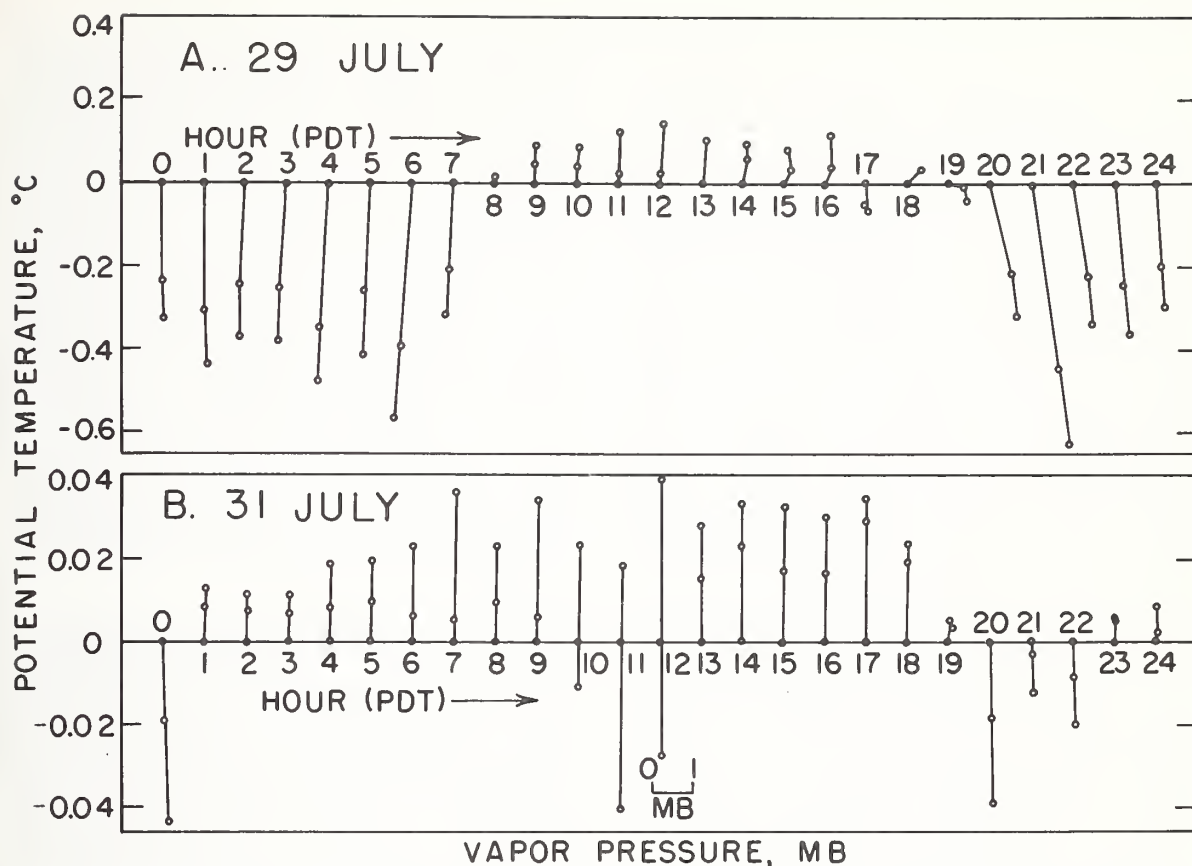


Figure 1. Similarity between gradients of potential temperature and vapor pressure. A. Clear weather on July 29, 1971. Levels 1, 4, and 6. B. Overcast weather on July 31, 1971. Levels 1, 2, and 3.

ment of Θ and e with respect to the first measurement level near the canopy.

Though several points can be deduced from such similarity plots, the most important conclusion concerns adequacy of data. The linearity at the selected levels confirms their acceptability for the Bowen ratio model, although an unexplained offset is evident at level 2 during the 1000-1200 hours on July 31.

Once the data is judged acceptable, one notes that the slope of the lines is $\Delta\Theta/\Delta e$; this is directly proportional to β , the Bowen ratio, as shown in equation 3. Thus the relative slope of the similarity plots is an index to the way that the surface is partitioning the net energy supply into convection and evaporation. Further, the quadrant of each hourly plot indicates the sign of β , and the direction

of the H and λE fluxes.

For example, as plotted in figure 1A and 1B, both fluxes will have the same sense in quadrants I and III where the slope is positive ($\beta > 0$). In quadrant I, H and λE are both directed away from the surface and are negative by the sign convention adopted earlier. In quadrant III, H and λE are both positive, as their sense is toward the surface. The slope and the β coefficient are negative in quadrants II and IV. In quadrant II, H is toward the surface (advection) while λE is directed away, while the fluxes in quadrant IV have the opposite sense. The similarity plots can thus provide three things: a ready indication of the magnitude of the Bowen ratio; an indication of the direction of the H and E fluxes; and an identification of levels suited for the Bowen ratio analysis.

Evaluation of Stored Heat

Application of the Bowen ratio model to forest measurements reveals a problem in measuring the stored heat term in equation 2 that is a direct consequence of the nature of the forested surface. The scale of the forest elements makes the change in heat storage in the biomass difficult to measure, and many studies (Baumgartner 1956) have treated these changes as negligible. This is certainly true on a daily basis, but an appreciable amount of energy appears to move into storage (-G) in the biomass in the early morning, and out again (+G) in the early evening. These amounts ordinarily will balance when totaled over the day, but comparisons among hourly totals may be in error unless the energy storage changes are estimated for the biomass as well as for the soil.

The estimates of biomass storage change were derived here by an indirect method that may prove useful in other situations as well. First, application of the Bowen ratio model to data collected during the early evening hours frequently resulted in positive estimates of latent energy (condensation) when the vapor gradient clearly indicated that evaporation was taking place. This apparent anomaly in the Bowen ratio estimate of λE could occur as a consequence of underestimating the storage term G. In order to obtain the proper sign on λE under these conditions, the estimate of G must be increased to a positive value that exceeds the absolute value of the negative net radiation.

Estimates of the minimum probable value of G were obtained in this manner for the hours between sunset and the time near midnight when the vapor gradient changed direction, indicating the beginning of condensation. As a second step, the crossover points between release (+G) and uptake (-G) of stored energy were then estimated from my experience and that of others (Gruliois 1968) as being about 1 hour after sunrise and 3 hours before sunset. The release of stored heat (+G) is then defined by the two crossover points and by the magnitude during the early evening hours. The third and final step was to estimate the magnitude of the gain in

storage (-G) during the morning hours so that the daily integral approximately balanced. The final result is a much better estimate of hourly changes in stored energy than could be obtained by direct measurement of the soil storage component alone. The magnitude of the stored energy change will be investigated further during future studies.

The major problems in application of the Bowen ratio model to the forest appear to be associated with adequate precision of the measurements. The similarity tests demonstrated here appear useful in eliminating errors from the data. Further, the changes in stored energy can be estimated by an indirect method, based upon gradient measurement and knowledge of the time at which the stored heat flux reverses sign.

The Forest Energy Budget

Energy budget analyses were developed for 2 days that represent quite different amounts of available energy. The solar energy input to the forest was large on July 29, 1971, a day characterized by clear skies and a warm mean temperature (24.4°C). In contrast, July 31, 1971, was completely overcast with reduced levels of incoming solar radiation and a relatively cool mean temperature (17.4°C). Examination of the energy budgets under such contrasting conditions will improve our understanding of the basic processes that govern energy transfer between the forest and the atmosphere.

The diurnal energy budget will first be examined with respect to daily totals; a discussion of the relationships among hourly values of the energy budget components will then follow.

The Diurnal Energy Budget

The daily energy budget totals are presented for the separate periods of daylight (13 hours) and night (11 hours) and for 24-hour totals in table 1. Dividing the daily totals into daylight and night portions enhances future comparisons that may be made with data collected under different daylengths at Cedar River or elsewhere.

Table 1.—Diurnal energy budget components¹

Period	July 29—clear				July 31—overcast			
	Q*	G	H	λE	Q*	G	H	λE
----- cal/cm ² -----								
Daylight	454	-43	-143	-263	141	-7	-38	-96
Night	-44	48	8	-17	-7	13	-1	-6
Daily total	410	5	-135	-280	134	6	-39	-102

¹Totals are given for the daylight hours, 0630-1930 PDT; night hours, 1930-0630 PDT; and the full day, 0000-2400 PDT.

There is a large difference in the radiation supply on the 2 days, as net radiation totaled 410 cal/cm² under the clear skies of July 29, and only 134 cal/cm² for the overcast conditions of July 31. These totals include a steady net loss of radiation at night, amounting to -44 cal/cm² under clear skies, and -7 cal/cm² under the overcast conditions.

The net radiation term represents the energy converted from radiative to nonradiative forms by the forested surface. The short-wave radiation from the sun makes up the largest component of the net radiation. During the 13 hours of daylight on the clear day, the forest received 584 cal/cm² of solar radiation and reflected 55 cal/cm². Under overcast skies, the forest received 171, and reflected 16, calories/cm². The albedo was 0.09 on both days.

Since the gain and loss of longwave radiation also enters into the supply of radiant energy, it is not helpful to calculate a short-wave/net radiation ratio as an index of efficiency of conversion. However, the low albedo value (0.09) emphasizes the efficiency with which the Douglas-fir canopy absorbs solar radiation. This low reflectivity is similar to values reported for other coniferous canopies (Stewart 1971), and is much lower than the 0.2-0.25 albedo values that commonly prevail over crops and other low vegetation (Monteith and Szeicz 1961). As noted by

Baumgartner (1971), forests are effective absorbers of solar radiation.

The changes in stored energy (G) tabulated in table 1 for the 24-hour period are near zero, which is in accord with observations reported elsewhere. This term represents the changes in heat storage of both the biomass and the soil. Most of the storage changes are attributed to the biomass; the indirect methods used to estimate the changes in storage have been described in an earlier section.

I estimate that -43 cal/cm² went into storage during the daylight hours on the clear day and that 48 cal/cm² came out of storage during the night. The storage changes on the cloudy day proceeded in a similar direction, but the magnitudes were much smaller.

The storage term at Cedar River appears large because of the large quantity of the biomass there. The biomass is as yet unmeasured, however. Attempts will be made to measure the storage flux directly in future experiments.

The convective flux for the clear day totaled -135 cal/cm², directed away from the forest into the atmosphere. A slightly larger amount, -143 cal/cm², was lost during daylight, but 8 cal/cm² was gained by the canopy at night when the canopy temperatures dropped below that of the air. Under overcast sky conditions, -38 cal/cm² were lost over the full day.

Latent energy was the largest dissipation term on each of the days, totaling -280 cal/cm^2 for July 29 and -102 cal/cm^2 on July 31. There was a net loss of latent energy by night, as well as by daylight, for both days. The evaporation equivalent of the latent energy total was about 0.5 cm on July 29, and 0.18 cm on July 31.

The Bowen ratio ($\beta = H/\lambda E$) is a measure of how the surface partitions the energy supply between sensible and latent heat. The mean daily value of β was 0.48 for the clear day, and 0.38 for the overcast day. The difference in β between days is not large, but it suggests that the forest partitioned more of the energy supply into convection on the clear day than on the overcast day. From another viewpoint, the ratio of $\lambda E/Q^*$ was 0.67 on the sunny day, and 0.76 on the overcast day. This is in the direction that one might expect for a stand of vegetation that receives a large input of energy.

Hourly Energy Budgets

The phase relationships among the energy budget components can be examined with the

aid of figure 2 which shows the hourly values on July 29, and figure 3 which shows the hourly values on July 31. Each plotted point represents the midpoint of an hourly mean. The daytime, night and daily totals in table 1 were integrated from the rates shown in these two figures. The 2 days exhibit different characteristics, so they will be discussed separately.

The symmetry of the bell-shaped net radiation curve on July 29 confirms that the skies were cloudless on that day. The maximum intensity occurred during the hour centered on 1300 hours PDT, which closely corresponded with solar noon. The net radiation values became positive about 1 hour after sunrise and remained positive until shortly before sunset, indicating the hours in which there was a surplus of energy that might be dissipated through the other energy budget components. The net radiation was negative throughout the night, as the surface lost energy to the atmosphere. The greatest net radiation loss occurred at 2200, about 1 hour after sunset at a time when the forest was rapidly losing the absorbed solar radiation that had been stored during the day.

The phase of the fluxes is also of interest,

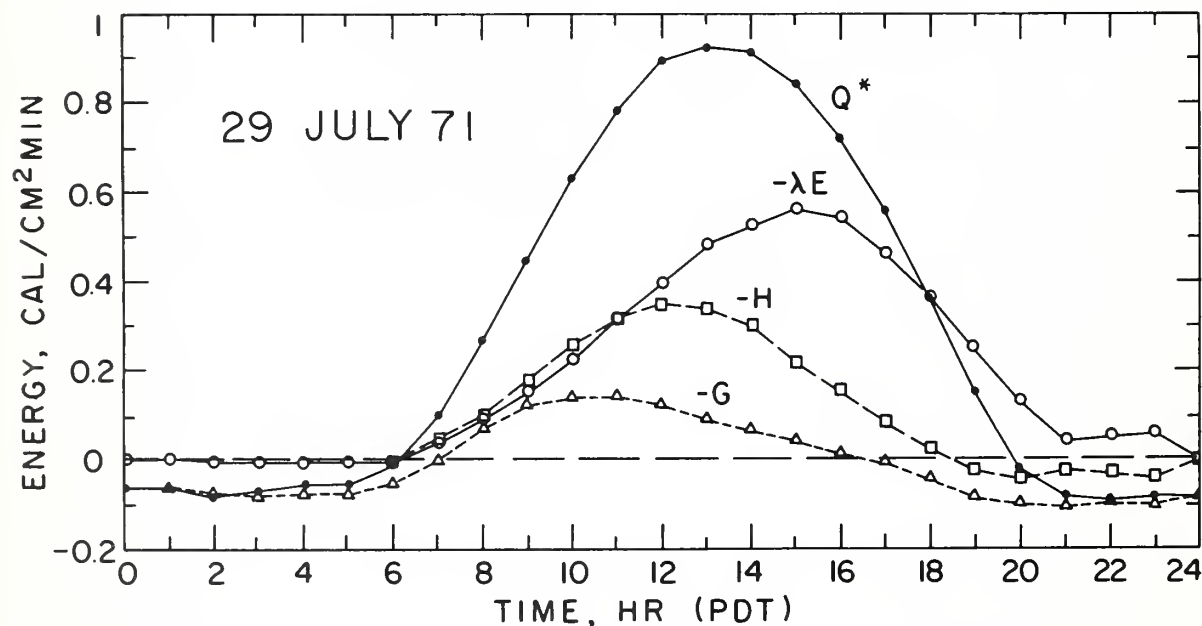


Figure 2. Energy budget components under clear skies. Symbols: net radiation, Q^* ; change in heat storage of soil and biomass, G ; convection, H ; latent energy, λE .

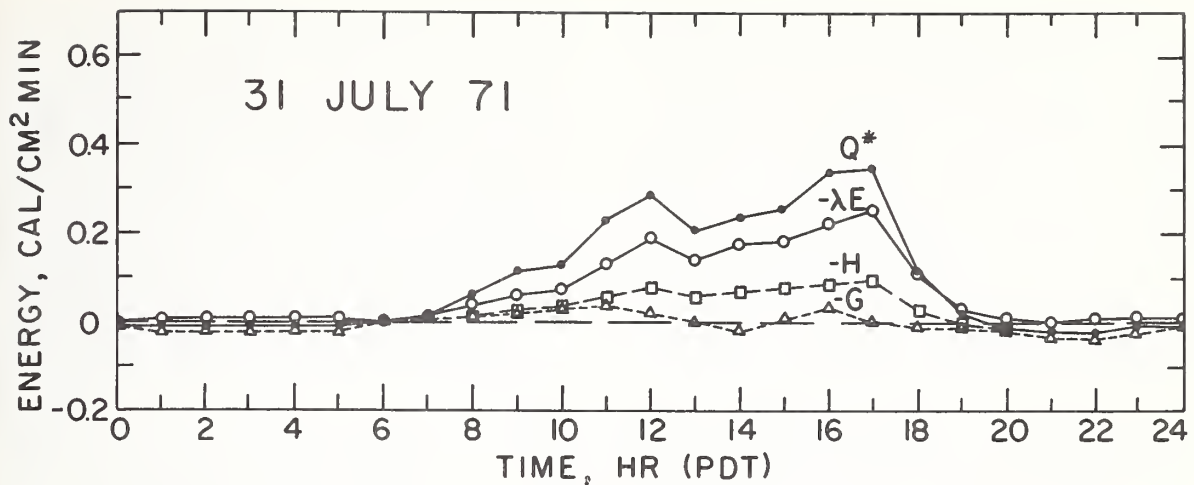


Figure 3. Energy budget components under overcast skies. Symbols: net radiation, Q^* ; change in heat storage of soil and biomass, G ; convection, H ; latent energy, λE .

as G , H , and λE all lag behind Q^* . Let us consider the stored heat flux first. It reaches its peak flow into the biomass and soil ($-G$) in midmorning, and reverses to flow out of the biomass ($+G$) in the late afternoon and early evening. The change in stored heat appears to provide a significant source of energy to the surface throughout the night.

The sensible heat flux, H , reaches its maximum about two hours after G , but still an hour before solar noon. Sensible heat is directed away from the surface during daylight ($-H$), but reverses in direction as convection begins to provide energy ($+H$) to the surface during the night. During this period, the canopy cools below air temperature due to longwave emission.

The latent energy flux reached its maximum about two hours after solar noon. Evaporation continued well into the night; only during the early morning hours did a rather small amount of condensation take place.

The marked phase shift between sensible and latent energy is of interest, as many studies have shown these two fluxes to be in phase with net radiation (Baumgartner 1956, Denmead 1969, Rauner 1960). The Douglas-fir forest, in contrast, partitioned the energy available at the surface into sensible and latent energy on a preferential basis. This partition was on a 1:1 basis during the morn-

ing, but latent energy was apparently favored at the expense of sensible energy during the afternoon. A similar pattern is evident in measurements over a young Douglas-fir forest near Vancouver, B.C. (Black and McNaughton 1971), and over a mixed hardwood forest (Gruliois 1968).

The phase shift in latent energy into the afternoon is probably related to a vapor pressure deficit which has an afternoon maximum on clear days. Stewart and Thom² have concluded that the latent energy flux from their pine forest site in England is controlled more by the vapor pressure deficit than by the supply of available energy. This conclusion is based upon their evaluation of the interplay between the relatively large internal resistance to transfer and a small external resistance; the ratio for the pine site was in the order of 20:1.

Conclusions

The observations reported here are an initial contribution toward the problem of evaluating the flow of energy and mass between the atmosphere and the young Douglas-fir forest at the Cedar River site.

²J. B. Stewart and A. S. Thom. Energy budgets in pine forest. Institute of Hydrology, Wallingford, Berkshire, U. K. Unpublished manuscript, 1972.

Forested surfaces are generally considered to be effective energy exchange surfaces. The results confirm that this young stand has a high absorptivity for solar radiation, with an albedo of 0.09 for both clear and overcast conditions. This high absorptivity contributes to the large net radiation values that were measured under clear skies.

The role of the forest in dissipating the net radiation is of particular interest. The porous, aerodynamically rough canopy is effective in transferring sensible and latent energy into the atmosphere. The large quantity of forest biomass may also involve an amount of stored thermal energy that is of significance during short periods, even though the daily totals are small. Summed over a 24-hour period, evapotranspiration was about $280 \text{ cal/cm}^2 \text{ min}$ (0.5 cm water equivalent) or about two-thirds of the net radiation that was transformed under clear skies. Evapotranspiration was relatively larger on an overcast day, about three-quarters of net radiation, although the total amount of latent energy ($102 \text{ cal/cm}^2 \text{ min}$, or 0.18 cm water equivalent) was considerably lower.

These results provide initial estimates of the amounts of energy transferred during extreme conditions under cloudless and under overcast skies. The exchange of energy and mass depends not only upon the energy input to the forest, however, but also upon the physiological response of the vegetation. Now that the instrumentation system and the analysis model have been tested at this site, subsequent research will include a range of environmental conditions. Instrumentation development and model testing will continue in cooperation with the lysimeter installation and eddy flux system of cooperating investigators. Ultimately, analysis and interpretation of the energy transfer studies must include physiological as well as physical characteristics of the stand.

Acknowledgments

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The lysimeter installation on the Cedar River Watershed

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Abstract

*A lysimeter was built around the root ball of a 28 m Douglas-fir (*Pseudotsuga menziesii*) tree. The container, tree, and soil weigh 28,900 kg. The sensitivity of the weighing mechanism is 630 g which is equivalent to 0.06 mm of water. The installation will be used to study evapotranspiration and volume changes in relation to soil water potential and atmospheric demand; to test cuvette and meteorological methods; determine canopy interception; and to assess the effects of irrigation and fertilization.*

Introduction

Understanding the process and quantifying the rate of water transfer within a forest ecosystem has become increasingly more important in recent years. This concern has originated from both applied and basic directions. For example, it has been estimated that by 1980, six major regions will have no water reserve. These regions are Colorado River, South Pacific, Great Basin, Upper Rio Grande, Pecos River, and Upper Missouri River (Colorado River Association 1966). Furthermore, interbasin transfer is being practiced in at least two areas at the present time.

Increasing need for water conservation, the possibility of interbasin water transfer, and the treatment of watersheds to increase yield or change quality has demonstrated the need for additional research on water use by various types of vegetative cover. For example, clearcutting a north-facing Coweeta watershed resulted in a 1st year increase streamflow of 40.2 cm and a stabilized increase of 23.8 cm. Although the 1st year's increase from a south-facing watershed was only 15 cm which de-

creased to insignificance by the 3d year (Swift, unpublished data), it is believed that the different microclimatic influences upon the vegetation and resulting evapotranspiration will account for the discrepancy in water yield. To understand fully the processes involved and to predict results from future cuttings require detailed investigations relating water use to its availability and to atmospheric conditions.

Short-period (1 hour or less) determinations of evapotranspiration are necessary to study the complex soil-plant-atmospheric relations. Many methods or combination of methods have been employed to determine evapotranspiration. The major ones include watershed runoff; measurement of soil moisture depletion by either gravimetric sampling, with resistance blocks, or with neutron soil moisture meters; use of weighing lysimeters; and application of meteorological models. Other methods have employed percolation tension plates, stemflow measurements, and enclosures. Of these methods only weighing lysimeters, enclosures, and meteorological models are capable of yielding hourly results. Enclosures alter the microclimate and

may bias the results. Meteorological methods must be tested in the areas of anticipated use (Slatyer and McIlroy 1961). Such testing has not been accomplished in forested areas. Thus, weighing lysimetry appears to be the only method capable of yielding the needed short period accurate rates.

Weighing lysimeters have been used to determine evapotranspiration of agriculture crops (McIlroy and Angus 1963, Pruitt and Angus 1960, Harrold and Dreibelbis 1951, Van Bavel and Meyers 1962), but they haven't been used for natural vegetation, such as brush and trees, which have extensive root systems.

The use of weighing lysimeters to determine evapotranspiration of trees is feasible only if the trees are uniformly spaced such as in a plantation. Installation is easier when the root system is naturally restricted, thereby reducing the size of the lysimeter and its deadweight. Under these conditions, it would be possible to obtain accurate short period evapotranspiration rates, thus enabling a mechanistic examination of evapotranspiration in relation to the determining meteorological and soil moisture conditions.

Establishment of evapotranspiration from a single tree or group of trees in a specific location is important but does not yield answers for other types of vegetation in different climatic zones. Installation of lysimeters in many locations is not possible and may not be feasible because of the cost. However, meteorological methods if tested can be employed to establish evapotranspiration rates where lysimeters are not feasible. Results from meteorological methods can be tested against the results from a properly installed weighing lysimeter. This has been accomplished for agriculture crops (Tanner 1967, Pruitt 1963, Fritschen and Van Bavel 1963, Fritschen 1965). However, differences in scale factors such as canopy height, density, and roughness demand additional testing before these methods can be used over natural vegetation.

The purpose of this paper is to discuss the establishment of the weighing lysimeter in a Douglas-fir forest for the primary purpose of studying the complex relation between evapotranspiration rates and the determining

meteorological and soil moisture conditions. In later stages the installation will be used to evaluate meteorological methods for determining evapotranspiration to be used in other areas.

The Site

The lysimeter installation is located on the Cedar River Watershed near Seattle, Washington. The soil is a Barneston, gravelly, loamy sand originating from glacial outwash laid down at the end of the Vashon glacial period (Poulson and Miller 1952) and generally restricts the root system above the 3-foot depth (Gessel and Cole 1965). The lateral extent of the root system is largely restricted to the basic spacing of the trees. The area is relatively level and has a uniform canopy density making it desirable for micrometeorological investigations.

The trees are 35-year-old Douglas-fir (*Pseudotsuga menziesii*) which regenerated naturally after logging. The average tree spacing is 5.8 m, resulting in 231 trees per 4,041 m² consisting mostly of Douglas-fir with a few hemlock (*Tsuga heterophylla*) and maple. Trees in the 5 to 30 cm d.b.h. classes occur with the greatest frequency. Ground vegetation consists of bracken fern (*Pteridium aquilinum*), salal (*Gaultheria shallon*), red huckleberry (*Vaccinium parvifolium*), and mosses, mainly (*Eurhynchium oregonum*).

The Lysimeter

The lysimeter was constructed around the root ball of a 35-year-old, 28 m tall and 38 cm diameter Douglas-fir tree. The lysimeter consists of two right cylinder containers, one located within the other. The innermost container in which the tree is located is 366 cm in diameter and 122 cm deep, having a surface area of 10.5 m² (fig. 1). The container at "field capacity" with tree and soil weighs 28,900 kg (fig. 2).

The inner container is resting on a hydraulic transducer located on the bottom of the outer container. The hydraulic transducer consists of eleven 15 m lengths of 6.35 cm



Figure 1. Walls of the inner container being fitted together prior to lowering down around the root ball.



Figure 2. Completed inner container with soil and tree shown raised 90 cm for installation of the hydraulic transducer.

butyl rubber tubing with a valve stem vulcanized 30 cm from one end. The tubing was filled with air-free water and was coiled on the bottom of the outer container starting at the center (fig. 3). Holes were cut in the bottom of the outer container to allow the valve stems to pass through. Thick-walled tubing (9.5 mm I.D.) was attached to each valve stem and extended beneath the bottom of the outer container to a shutoff manifold. The manifold is connected to a vertical standpipe; thus, the weight of the tree, soil, and inner container is reflected in the height of the water column in the stand pipe. A water-filled dummy standpipe is located adjacent to the



Figure 3. Butyl rubber tubing used for weighing coiled on the bottom of the outer container.

active standpipe for the purpose of temperature compensation and counter balance. Weight changes are detected by a ± 6.9 mb differential pressure transducer located between the active and the dummy standpipes. The signal is recorded on an automatic data logging system.

To provide for drainage of excess water, eight filter candles were installed around the periphery of the inner container about 10 cm from the bottom. The filter candles were 5 cm in diameter by 20 cm ceramic tubes with a bubbling pressure in excess of 250 millibars. The filter candles are connected through a manifold system to an evacuated reservoir. The outflow from the drainage system is measured with a modified type tipping bucket rain gauge.

To prevent the tree from blowing or falling over during and after construction, it was guyed from a yoke located at 10 m to the base of adjacent trees. After construction four climbable (30 cm triangular) towers were built around the lysimeter and the tree guyed to the towers with horizontal cables. The cables were loose enough to allow 15 cm motion at 10 m.

The sensitivity of the lysimeter is 630 g which is equivalent to 0.06 mm of water or 22 ppm. The lysimeter installation at Tempe, Arizona (Van Bavel and Meyers 1962), has a sensitivity of 20 g or 0.02 mm of water or

7.4 ppm. The lysimeters at Coshocton, Ohio (Harrold and Dreibelbis 1951), have a sensitivity of 2,268 g or 0.25 mm of water or 38 ppm and the lysimeter at Davis, California (Pruitt and Angus 1960), has a sensitivity of 907 g or 0.03 mm of water or 20 ppm.

The Weather Station

Located adjacent to the lysimeter tree and on a tower 33.5 m in the air are the meteorological sensors of the weather station. These consist of a solarimeter, a net radiometer, air temperature sensor, vapor pressure sensor, wind direction and speed sensors, and a tipping bucket rain gauge. In addition to these parameters, soil temperature is measured at four depths inside and outside of the lysimeter. The signal from these sensors is recorded automatically on a digital magnetic tape data logging system. At the present time, five of the signals are being integrated continuously: solar radiation, net radiation, rainfall, windspeed, and the drainage from the lysimeter. The integrals of these signals and the other parameters are recorded on the magnetic tape at hourly intervals to conserve the magnetic tape's supply. With hourly records, the tape supply will last for 30 days. The magnetic tape (6.4 mm) is converted to 12.7 mm computer compatible tape and then analyzed at the University of Washington Computer Center with the Burroughs 5500 computer.

The Proposed Uses of the Lysimeter Facility

Since the lysimeter was installed during the summer of 1970 and the completed facility was not completely checked out until recently, very little data is available for discussion. However, it may be enlightening to discuss the proposed uses of the facility.

An Evapotranspirimeter

The lysimeter installation is expected to

yield short period rates of evapotranspiration from the 28 m Douglas-fir tree. The accuracy of the measured evapotranspiration is without much question. How representative the data are is questionable unless the water potential of the root mass is kept equal to the water potential of the root mass of adjacent trees. Since the root mass is restricted in a 366 cm diameter container, the amount of soil available for water and nutrient extraction by this tree is slightly less than adjacent trees. During the summer months, water should be withdrawn from the lysimeter container at a faster rate than from the adjacent soil. Therefore, water will have to be added to the lysimeter container to maintain a water supply equal to that in the adjacent area. During the winter months, the opposite will be true. The bottom of the lysimeter container inhibits deep percolation. When rainfall exceeds evapotranspiration, water will have to be removed from the container in order to prevent a buildup of water in the bottom of the container.

Evapotranspiration as a Function of Potential

In order to study the mechanism of transpiration from a Douglas-fir tree, the evapotranspiration rates will be determined in relation to the soil-water potential and the atmospheric evaporative demand. During these studies, soil moisture potential will be determined with a series of thermocouple psychrometers installed in the lysimeter container. The atmospheric evaporative demand will be calculated from meteorological parameters.

Tissue Volume Changes

Dendrometer bands will be installed at various locations on the tree to study the swelling and shrinking of the tree in relation to water potential and evapotranspiration. At the same time, stomata aperture and plant stress will be determined using leaf resistance meters and thermocouple psychrometers or Scholander bombs.

Test Cuvette Technique

While the detailed studies of evapotran-

spiration are being conducted, cuvettes will be installed at various locations within the crown to monitor the spacial variation of transpiration. In addition, the rates of transpiration, determined with the cuvettes, will be compared with the lysimetric transpiration rate to determine how representative the cuvette technique is for determining transpiration of the tree.

Test Meteorological Methods

Meteorological methods such as energy balance, aerodynamic, and eddy correlation techniques have been used to determine evapotranspiration from agriculture crops. The methods need further testing in forestry before they can be utilized on a wide scale. The evapotranspiration rates from the lysimeter tree, if representative of other trees, can be utilized for testing the meteorological methods.

Profiles of meteorological parameters such as radiation, temperature, humidity, carbon dioxide, and windspeed will be monitored. These parameters will be utilized to calculate the transfer coefficients (eddy diffusivities) of sensible heat, latent heat, momentum, and CO_2 . In addition, transpiration and photosynthesis by layers will be calculated from these parameters.

Canopy Interception of Precipitation

Interception of precipitation either as rain, dew, or snow will be represented as a weight increase by the lysimeter. The amount of precipitation intercepted by the crown of the tree can be studied by providing a waterproof cover for the soil surface to prevent the throughfall from being recorded as a weight increase. The throughfall will be measured separately. If stemflow is measured, then the rest of the weight increase can be attributed to canopy interception. It is obvious that this method can be utilized to determine the amount of rainfall and snowfall interception in relation to intensity, duration, and previous wettings.

However, this technique may be more useful in determining the amount of moisture

extracted from the atmosphere as dewfall—at present, an unknown quantity. During the summer months, energy budget calculations demonstrate that Douglas-fir trees, under the conditions of the site, would be stressed within 2 to 3 weeks after the last rainfall if they transpired at a potential rate, unless transpiration is supplemented by evaporation of dewfall. Dewfall may be a very important parameter in the survival of these trees.

Fertilization and Irrigation

At the present time considerable interest is being expressed in using forested areas for disposal of sewage sludge. The benefit of irrigation, sludge, or other fertilizers to tree growth could be tested with the lysimeter installation by comparing the photosynthesis and transpiration of the tree being studied with the adjacent trees.

Summary

During the summer of 1970, a lysimeter container (366 cm in diameter and 122 cm deep) was built around the root mass of a 28 m Douglas-fir tree at the Cedar River Watershed near Seattle, Washington. This container was placed on top of the hydraulic transducer which is capable of weighing the tree, soil, and container, a mass of 28,900 kg, with a sensitivity of 630 g or 0.06 mm of water. A weather station was located on a 33.5 m tower adjacent to the lysimeter tree.

The proposed uses of this installation are: (1) as an evapotranspirimeter, (2) as a standard for testing cuvettes, (3) as a standard for testing meteorological methods, (4) to study evapotranspiration in relation to soil moisture potential and atmospheric evaporative demands, (5) to study the shrinking and swelling of the plant tissue in relation to evapotranspiration, (6) to determine interception of rainfall, snow, and dewfall by the crown, and (7) to study the effects of irrigation and fertilizer upon the growth of the tree.

Acknowledgments

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Initial steps in decomposition of Douglas-fir needles under forest conditions []

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Abstract

Douglas-fir (Pseudotsuga menziesii) needle decomposition was evaluated after 6 and 12 months exposure to forest floor conditions by characterizing solubility changes of saccharides, waxes and oils, and cellulose. The results lead to the hypothesis that primary processes of decomposition are initiated on the outside of the needle with the solubilization of waxes and, as the waxes are depleted, the cellular constituents are solubilized.

Introduction

Approximately 4 percent of the biomass of the Douglas-fir consists of needles (Dice 1970) containing a portion of the carbon to be cycled within the ecosystem. Some genera of the Moniliales have been reported that are capable of utilizing cellulose and breaking down needle waxes to release carbon (Macauley and Thrower 1966; Martin and Juniper 1970). The decomposition of needle litter and the release of carbon in a forest is important in the nutrient cycling processes within a conifer ecosystem. In an effort to study carbon cycling pathways and the part played by the processes of the decomposition of Douglas-fir needles the following investigation was conducted.

Primary decomposition is defined as changes in solubility of the needle constituents. Therefore to study decomposition techniques were used to detect changes in solubility. Simplistically, needles consist of an outer layer of cutin and waxes and an inner cellular layer made up of cellulose and protoplasmic contents. Needle constituents were divided into three classes: (1) compounds extractable with hexane (primarily cuticle waxes) (Martin and Juniper 1970), (2) those

extractable with hot water (saccharides) (Campbell 1952), and (3) cellular components soluble in 1 percent HaOH (hemicellulose) (Campbell 1952).

Materials and Methods

Needles used in this study were collected in the following manner. Screen traps were attached to a tower at random intervals in height from just below the crown of the trees to ground level. Needles were collected from the traps aseptically, placed in sterile containers, and transported to the laboratory for analysis and further study. In addition needles from the traps were placed in nylon mesh bags on the forest floor and allowed to decompose. After exposure for 6 and 12 months the needle samples were analyzed in the following manner.

Samples were oven dried for 24 hr. at 105°C and stored in airtight containers until analyzed.

Three 8-g replications of each treatment sample of needles were extracted with boiling n-hexane in a Soxhlet extractor for 6 hr. and oven dried for 24 hr. at 105°C to remove the hexane and weighed. The amount of material

extracted was determined by the weight differences before and after extraction.

Water soluble materials were determined in a similar manner using boiling water.

As employed by Cowling (1961), a 1 percent NaOH solubility test was used to determine rate of cellulose decomposition.

In an effort to isolate fungi involved in the decomposition processes needles were cultured in two ways: A portion of each sample was plated on 2 percent malt extract agar and onto an antibiotic medium consisting of 2 percent malt extract agar plus 1:30,000 Rose Bengal and 50 p.p.m. streptomycin. A second portion of each sample was washed in sterile water for 2 minutes and the needles plated onto these same agars. The plates were incubated at 26°C for 7 to 14 days. Isolations were made from the resulting fungi.

Results

Table 1.—Frequency of occurrence of genera of fungi isolated from needle samples

Months	Genera	Frequency of isolation ¹
0	<i>Phomopsis</i> sp.	4
	<i>Mucor</i> sp.	2
	<i>Penicillium</i> spp.	2
	<i>Trichoderma</i> spp.	2
	<i>Botrytis</i> sp.	1
	<i>Graphium</i> sp.	1
6	<i>Phomopsis</i> sp.	2
	<i>Mucor</i> sp.	3
	<i>Penicillium</i> spp.	4
	<i>Trichoderma</i> spp.	4
	<i>Aspergillus</i> spp.	3
12	<i>Penicillium</i>	4
	<i>Trichoderma</i> spp.	4
	<i>Mucor</i> sp.	4

¹ 1 = Very infrequent
2 = Infrequent
3 = Frequent
4 = Very frequent

Discussion

Several genera of fungi have been reported to exhibit the capability to utilize waxes (Martin and Juniper 1970). From the data in figure 1 it appears that fungal action on the needle waxes causes these materials to become more soluble in hexane after a period of time. There is a large weight loss in hexane extractables after a six month period and a smaller weight loss after 12 months. It appears from this trend that during the first 6-month period, waxes are acted on initially during primary processes of decomposition. This was followed during the second 6-month period by the processes of increasing solubilization of cellulose and saccharides.

Dice (1970) reported that annual production of organic matter for Douglas-fir litter is 359 kg/ha. The density data in figure 1 shows that at 12 months there is a 60 percent reduction of organic matter or approximately 213 kg/ha.

The fungi listed in table 1 are being studied to determine what role they play in the physiochemical processes illustrated in figure 1.

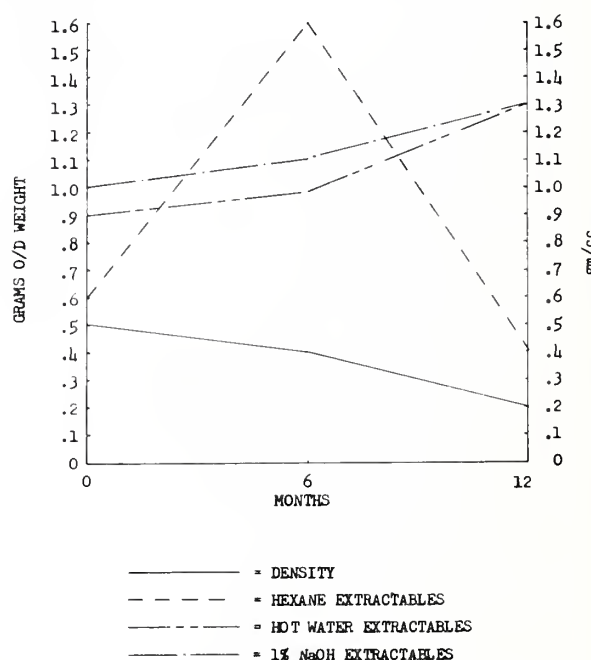


Figure 1. Density and weight loss of extractables of Douglas-fir needles after decomposition.

These preliminary results suggest the following hypothesis. Initially the primary processes of decomposition occur on the surface of the needle with the decomposition of waxes, and as the waxes are depleted, the cellular constituents are acted upon.

Acknowledgments

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Seasonal and diurnal patterns of water status in Acer circinatum

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Abstract

Diurnal patterns of water status were monitored in *Acer circinatum* on clear days during the summer of 1971. Sap velocity, branch water potential, and relative leaf resistance to water vapor diffusion were used to characterize the water status of a typical tree clump. Within the clump studied, air temperature and relative humidity were measured and used to calculate atmospheric vapor pressure deficits. Daily potential evaporation and soil moisture were calculated from U.S. Weather Bureau precipitation and air temperature data using the Thornthwaite method. Results suggest that the seasonal course of plant water status is dependent upon changes in soil moisture levels, possible changes in leaf morphology, and differences in diurnal patterns of water status resulting from differences in atmospheric moisture demand.

Introduction

Vine maple, *Acer circinatum* Pursh, is a major subordinate species within the Coniferous Biome ranging from the southern mainland coast of British Columbia to the coastal section of northern California. It is seldom found growing with a single stem; rather, it grows in clumps, forming a bushy mass. It is very shade-tolerant and is usually found under a tree canopy (Lyons 1964, Anderson 1968). Despite the prevalence of vine maple in this area, it seems that little is known of its physiological processes.

Numerous authors have illustrated the controlling influence of internal water regimes on physiological processes such as photosynthesis, respiration, translocation, and growth of forest trees and herbaceous plants (reviewed by Crafts 1968, Gates 1968, and

Zahner 1968). Also, transpiration, resulting in water loss from the soil, influences the total hydrologic cycle and water balance of forest stands (Rutter 1968). Therefore, understanding the water relations of a major subordinate species, such as vine maple, may be quite important to the study of productivity and water balance of forests within the Coniferous Biome. This study investigated diurnal patterns of internal water status in vine maple during the summer of 1971. Besides supplying general information on the water relations of vine maple, the study also supplied basic data which will be used in the development of a plant water status submodel for the Coniferous Biome. The data presented are also representative of some of the types of data presently being collected for conifers within the Biome (Walker et al. 1972).

Methods

The study was conducted at the Allen E. Thompson Research Center located about 55 km southeast of Seattle at an elevation of about 120 m in the foothills of the Washington Cascades. The Research Center is about 24 ha in size and is located on the western portion of the Cedar River watershed, in a 40-year-old second-growth Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, plantation. Dominant trees are about 24 m in height. Principal subordinate species, besides vine maple, are salal, *Gaultheria shallon* Pursh, Oregon grape, *Berberis nervosa* (Pursh) Nutt, sword fern, *Polystichum munitum* (Kaulf.) Presl., bracken fern, *Pteridium aquilinum* (L.) Kuhn var. *pubescens* Underw., and various species of moss. The climate is typical of lower elevations in western Washington. The average temperature in July is 16°C and in January, 3°C; the average annual precipitation is about 145 cm, with the majority falling during the winter months. The soil is a gravelly, sandy loam derived from Pleistocene glacial outwash. The vegetation, climate, geology, and soils in this area have been more completely described by Cole and Gessel (1968).

In the vine maple clump investigated, there were eight live stems, averaging about 3.7 cm in diameter at breast height. Since the stems were quite supple, a spreading crown form resulted with stem lean in all directions. This straggly, crooked form is common for vine maple growing in the shade (Lyon 1964). The tallest erect stem in the clump was about 10 m high. The clump was a moderately heavy Douglas-fir canopy.

The water status of the clump was characterized by measurements of sap velocity, branch water potential, and leaf diffusion resistance. Sap velocity of one major stem in the clump was estimated using a heat pulse velocity (HPV) meter and techniques described by Hinckley (1971). Numerous investigators have shown that HPV is a valid indicator of relative changes in the transpiration rate of forest trees (Skau and Swanson 1963, Wendt et al. 1967, Hinckley 1971). Readings were taken automatically every half hour and sap velocities calculated as described

by Marshall (1958). Branch water potential (ψ_b) was estimated using the pressure chamber apparatus and techniques described by Scholander et al. (1965). Many investigators have successfully used this technique to estimate ψ_b of trees in the field (Waring and Cleary 1967, Klepper 1968, Hinckley and Scott 1971). In this study, pressure chamber readings of at least three twig samples were taken and averaged for each observation period during the day. Samples were obtained from shaded portions of the crowns between the heights of about 0.5 and 2.5 meters. Each sample had at least two leaves attached to the twig. Leaf resistances (R_L) to water vapor diffusion (transpiration) were measured with a leaf resistance meter and techniques described by Van Bavel et al. (1965). Resistances were calculated using the meter sensitivity to temperature relationship described by Van Bavel et al. Therefore, though the readings proved to be adequate in indicating relative diurnal differences, their absolute magnitudes may be in error by a constant amount. Resistances for two or three intact vine maple leaves (obtained from similar locations as ψ_b samples) were measured and their values averaged periodically during the day.

Early morning and evening readings were usually impossible because of the very high resistances involved causing serious errors in measurement (Van Bavel et al. 1965). Probably, these high resistances are primarily due to nearly complete stomatal closure during these periods. Readings of HPV, ψ_b , and R_L were taken between about 0600 and 1600 Pacific Standard Time (PST).

Within the clump studied, relative humidity and air temperature (T_a) were measured in the shade with a sling psychrometer approximately every hour between about 0600 and 1600 PST. These data were used to calculate the vapor pressure deficit (VPD) of the atmosphere. Daily potential evaporation (PE) and daily soil moisture (SM) in the top 90 cm of soil were calculated for July, August, and September from precipitation (P) and air temperature data by the Thornthwaite method (Thornthwaite and Mather 1957) as modified by Machno (1966). The data used in these calculations were taken from the clima-

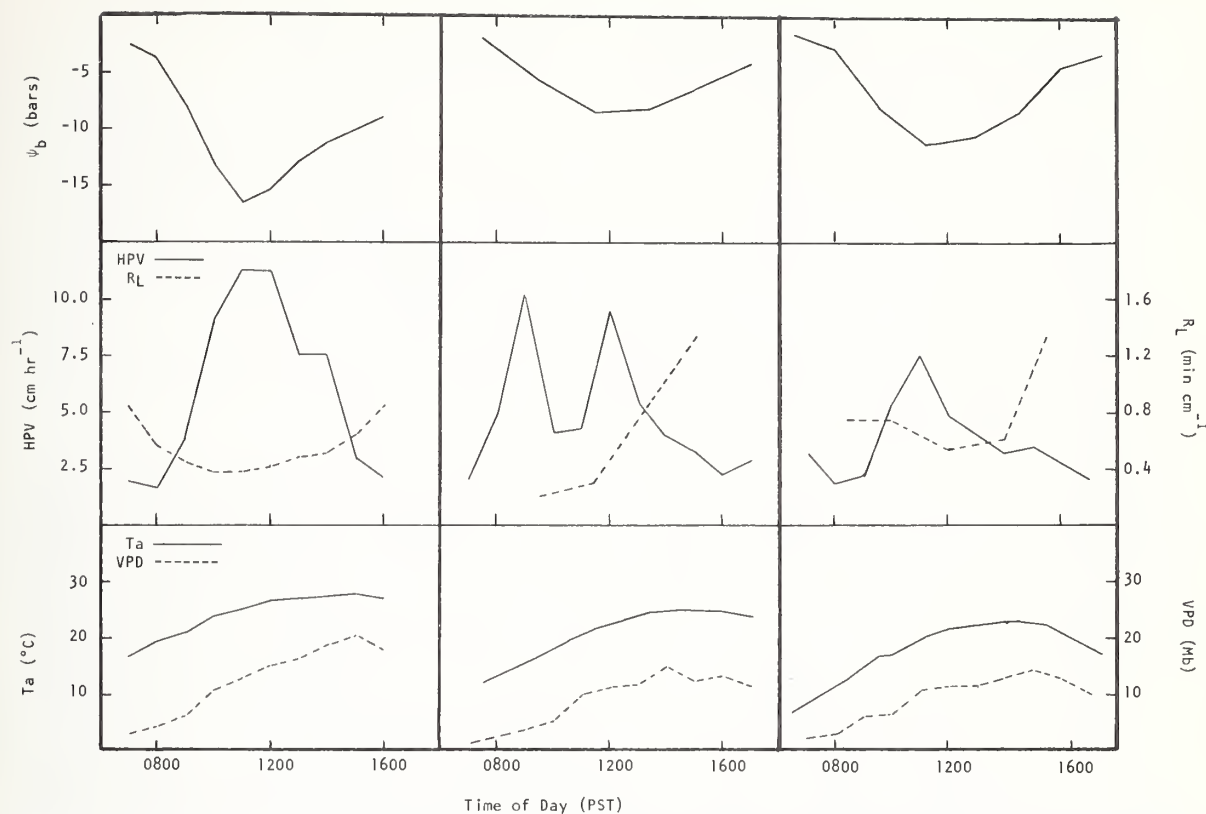


Figure 1. Daylight patterns of branch water potential (ψ_b), heat pulse velocity (HPV), leaf resistance (R_L), air temperature (T_a), and atmospheric vapor pressure deficit (VPD) for July 21, August 22, and September 22, 1971, at the Thompson Research Center, Washington.

tological records of the U.S. Weather Bureau Station at Landsburg, Washington, located about 3 km west of the Research Center at approximately the same elevation.

Results and Discussion

Water status and environment data examined in this paper represent typical data collected on clear days during the summer of 1971. The days presented as examples are July 21, August 24, and September 22 (fig. 1). An expected overall pattern for plant water status on these days is discernible in the results. During the early morning "predawn," the air was cool and fairly humid; R_L was high suggesting that stomata were relatively closed; ψ_b was high while HPV was quite low. As the day progressed, T_a increased, thus increasing VPD and intensifying the evaporative

demand. As stomata began to open, probably in response to increasing light levels, R_L values began to decrease. Since VPD had increased and stomata had begun to open, the tree began to transpire causing an increase in HPV readings. Continued water loss resulted in a decrease in ψ_b until about midday. In the afternoon, R_L increased because of stomatal closure probably due to decreasing ψ_b . With this came a corresponding decrease in HPV and an increase in branch water potential.

The summer was marked by an abnormally wet June, with more than 10 cm of precipitation having fallen. A rainless period followed during most of July and August; only on 1 day, August 21, did P surpass PE (fig. 2). The drought ended with a rainy period during the first 2 weeks of September. This was followed by 2 weeks without rain before another storm occurred near the end of September. The dry period during July and August produced a

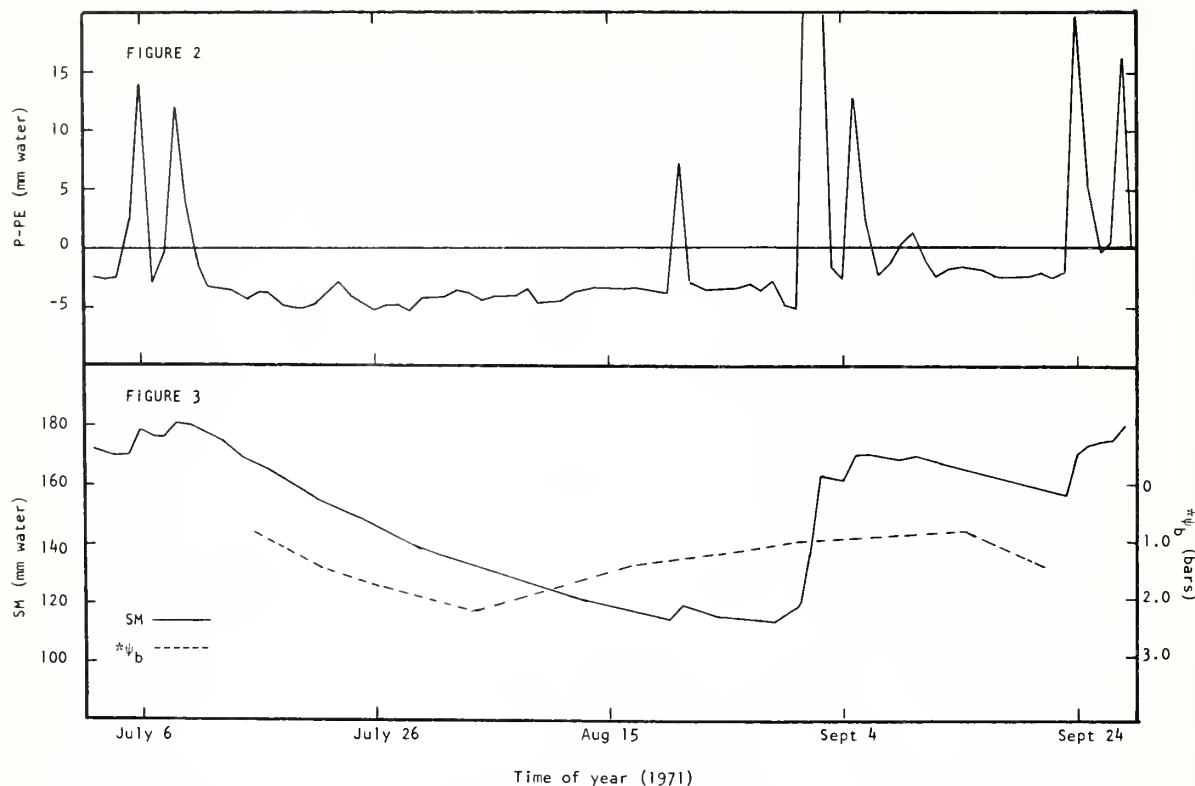


Figure 2. Precipitation minus potential evaporation (P-PE) calculated by the Thornthwaite method for July, August, and September 1971 at the Thompson Research Center, Washington.

Figure 3. Soil moisture (SM) in the top 90 cm of soil calculated by the Thornthwaite method and "predawn" branch water potential ($*\psi_b$) for July, August, and September 1971 at the Thompson Research Center, Washington.

steady drying of the soil from field capacity to a water potential well below -1.0 bar (fig. 3). The rain in early September recharged the soil to a point near field capacity. For the top 90 cm of this soil, field capacity is near 17.7 cm of water while the -1.0 bar point is about 14.2 cm (Knutsen 1965).

Since plants obtain water primarily from the soil and lose water to the atmosphere, their internal water status will depend greatly upon the SM supply and the atmospheric demand. The relationship of plant water status to SM is illustrated by examining "predawn" branch water potential ($*\psi_b$) periodically throughout the study period. These measurements were taken just prior to sunrise when ψ_b is usually the highest of the day and should most accurately reflect soil water po-

tential (Slayter 1967, Klepper 1968, Waring 1969). Therefore, a continuous decrease in $*\psi_b$ should have occurred during the rainless period in July and August because of the steadily decreasing SM (i.e., decreasing soil and water potential) during this period. Quite the opposite was observed (fig. 3). During the period, "predawn" branch water potential decreased steadily to a minimum on August 3 and then continually increased through August. This was surprising as $*\psi_b$ seemed to respond quickly to any change in SM, as illustrated by the immediate decrease in ψ_b during the temporary rainless period in September. Also, maximal and minimal points within this general trend proved to be significantly different at the 1-percent level (table 1). The apparent anomaly is probably explainable if

Table 1.—Tukey's w Multiple Comparison Test for seasonal "predawn" branch water potentials (ψ_b) showing significant differences at the 1-percent level. Values underlined are not significantly different.

Date	7/15	9/15	8/24	8/31	8/17	8/22	7/21	7/27	8/3
ψ_b	0.8	0.8	1.2	1.0	1.4	1.4	1.4	1.7	2.2

certain plant and environmental changes which occurred through the summer and which decreased daily transpirational water losses are taken into account.

The differences in daily plant water status which occurred on clear days during the study period would help explain the ψ_b trend observed (fig. 1). These differences seemed primarily due to a general decrease in the atmospheric demand through the study period (fig. 2). Generally, higher average T_a 's and VPD's and higher PE's occurred earlier in the summer, despite higher SM levels. A higher evaporative demand produced higher average HPV's and greater water loss, thus developing lower branch water potentials. The later part of August was marked by relatively lower T_a 's, VPD's and PE's, even though SM had decreased. Hence, lower transpirational losses occurred and higher ψ_b developed. During this period, a general increase in diffusion resistance was also evident.

It is also possible that changes in leaf morphology during the summer could have helped produce a trend of increasing ψ_b during a period of continually decreasing SM. Chlorosis in leaves, leading to necrosis before abscission, has been shown to be induced by drought, vascular disease, and normal senescence in woody and herbaceous plants (Kramer and Kozlowski 1960, Talboys 1968). Such manifestations, characteristic of "drought hardening" in plants, can produce decreased transpiration and photosynthesis rates due to persistent stomatal closure even while leaves are fully turgid (Talboys 1968, Turner 1969). By the

middle of August, the leaves of the vine maple clump investigated had developed numerous chlorotic spots; necrosis became evident during September. Therefore, increasing ψ_b during August could have been influenced by the systematic reduction in transpiration in portions of the leaves.

Conclusion

The diurnal patterns of water status in vine maple were examined for clear days during the summer of 1971. As expected, the seasonal pattern of plant water status was dependent upon a combination of certain soil, plant, and atmospheric factors which affected water uptake and loss by the plants. Soil water potential, which steadily decreased during the rainless periods, should have progressively limited water availability and resulted in the development of lower "predawn" plant water potentials. However, during a continuous drying cycle, changes in certain plant and atmospheric factors seemed to influence water loss greatly. Early in the summer, greater water losses occurred due to higher evaporative demands, and the plants were unable to recharge fully during the night even though adequate soil moisture was probably available. The development of chlorotic spots suggested that during a prolonged drought, or as the leaves approached abscission, the ability of the entire clump to transpire decreased. Also, as the atmospheric demand lessened later in the summer, less water loss occurred

during the day. Therefore, despite low soil water supply, greater nighttime recharging was possible because the deficits developed were less.

Acknowledgments

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Development and testing of an inexpensive thermoelectrically cooled cuvette []

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4045

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Abstract

*An economical temperature-controlled cuvette system has been developed to monitor CO₂ assimilation and dark respiration in the crowns of mature Douglas-fir (*Pseudotsuga menziesii*) trees at the Cedar River Thompson site. Temperatures in the Plexiglas assimilation chambers are controlled with thermoelectric coolers, and CO₂ concentration changes are measured with a differential infrared gas analyzer. Preliminary field data suggest cuvette temperatures can be maintained within $\pm 1^{\circ}\text{C}$ of ambient even under high insolation conditions.*

Introduction

The "cuvette technique" has been used for field assessment of [carbon dioxide assimilation] since the 1930's (Bosian 1933), but the findings of these studies have often been criticized. These criticisms of cuvette methods have usually resulted from the difficulties of maintaining a plant-chamber environment closely approximating that outside the enclosure.

Cuvette Problems

Problems encountered have included the development of "deep" boundary layers along leaf surfaces with the concomitant establishment of abnormal CO₂, vapor pressure, and temperature gradients. Additionally, CO₂ concentrations deviating markedly from ambient levels have frequently occurred and water condensation in chambers and in air conducting lines has been of particular con-

cern at night, during cold weather periods, and during periods of intense thermoelectric cooling of cuvette bases. But probably the most difficult problem to overcome has been that of chamber heating during periods of high insolation. In efforts to achieve temperature control under these conditions, a variety of chamber designs, fabrication procedures and materials, and cooling techniques have been utilized.

A common practice employed by many investigators has been the use of various thin plastic film "skins" to cover cuvette frames. Bourdeau and Woodwell (1965) used 8 mil polyvinyl chloride (PVC), Ritchie (1969) used 2 mil PVC, and Hodges (1965) used 5 mil polypropylene. These efforts have met with varying degrees of success because plastics differ markedly in CO₂ permeability, as well as infrared and visible light transmittance. As an example, though the IR transmissivity of polyethylene is relatively good its visible light transmittance is less than that of either Plexiglas (methyl methacrylate) or PVC. It is also

permeable to both CO₂ and water vapor. On the other hand, visible transmittance of Plexiglas and PVC is very good while PVC infrared transmissivity is better than Plexiglas and glass, though not as good as that of polyethylene.

Other methods of reducing temperature buildups have included the rapid conduction (700 - 1,500 l hr⁻¹) of air through assimilation chambers (Lerch 1965) and the circulation of water, water-ethanol, or water-ethylene glycol solutions through transparent jackets surrounding them.

Lange's (1962) and Ritchie's (1969) "Klapp-Kuvettes" were attempts to reduce temperature increases by alternately opening and closing the chambers during experimental periods. Ritchie observed air temperature buildups of 5° to 7° C and leaf temperature increases of up to 17° C when his cuvettes were closed. By alternately opening and closing them, these overtemperatures could be reduced by more than 50 percent.

Currently, the most convenient method of achieving cuvette temperature control appears to be through the incorporation of thermoelectric coolers into chamber designs. Using the Peltier principle to regulate temperature, Siemens Corporation (Erlangen, Germany) has manufactured a highly reliable and sensitive temperature and humidity controlled system whose utility and flexibility have been demonstrated by Schulze (1970). However, cost per unit prohibits Biome acquisition of a sufficiently large number for simultaneous sampling of CO₂ exchange in different crown locations, on different age classes of foliage, or on different plants. Therefore, routine monitoring must be accomplished with a less expensive system, reserving the Siemens equipment available for "factors studies."

Prototype Development

To complete a thorough daily and seasonal sampling program which will provide sufficient data to describe assimilation, dark respiration, and transpiration in representative individual Douglas-fir (*Pseudotsuga menziesii*) at the Cedar River Thompson site, a system composed of several reasonably priced cooled

cuvettes is considered highly desirable. As the first step in producing a functional system, a single prototype "two cuvette-power supply-temperature controller-fan controller" package (fig. 1) was fabricated from materials costing approximately \$675.

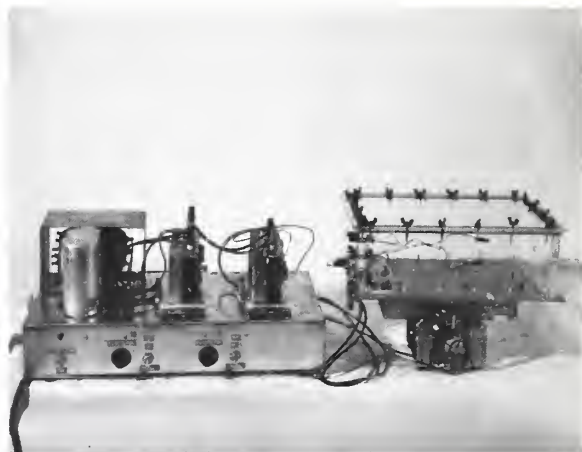


Figure 1. Prototype cuvette, power supply, temperature controller, fan controller package.

Two 5-liter chambers constructed of 3/8-inch Plexiglas are fitted with 1/8-inch aluminum bases, removable tops, and small 0-6 volt d.c. fans to mix the air and prevent boundary layer buildups. The aluminum floor of each chamber is securely bolted to the cold plate of an 80 watt Cambion (Cambridge, Mass.) Model 7250-1 "Forced Convection Thermoelectric Assembly" (TEA). The Model 7250-1 coolers operate in a range between 0 and 18 volts and 0 to 6 amps (larger TEA's are also available) and are powered by d.c. supplies each of which provides power for two cuvettes, two fans, two temperature controllers, and two thermoelectric coolers. Each control circuit has been developed around a temperature sensing silicon resistor (sensistor) bridge (originally diodes fashioned from transistors were used as temperature sensors), the imbalance in which determines the current output to the thermoelectric device.

Experimental System

Summer field trials for the cuvette were conducted at the Allen Thompson Research Center during 1971. The open system (fig. 2) utilized included an air intake approximately 25 m above the ground on a tower located 3 m from that used as an access to study trees. Air was drawn to the ground, through a 20-liter "mixing reservoir," to assure uniformity and prevent "noisy" carbon dioxide analyzer output, and then passed through a manifold for distribution to two Model 506R Reciprotor (Copenhagen) pumps. One of these pumped a comparison airstream to the URAS II (Hartmann and Braun, Frankfurt) infrared gas analyzer housed 46 m away in the permanent site building and the other moved air to the cuvette located at 17.2 m, back to the ground, through a flow meter, and then to the differential analyzer. The attenuating reservoir, manifold, pumps, and flow meter were located in a shelter at the tower base as was the power supply-temperature controller-

fan controller. A Honeywell recorder and the URAS II, however, were located in the site building. Two 0.004-inch copper-constantan thermocouples were used for temperature sensing inside the cuvette and one 22-gage thermocouple was positioned in a shaded location outside.

In addition to cuvette data, meteorological data were provided by instruments located on the adjacent meteorological tower. Scholander bomb and pressure infiltrometer (Fry and Walker 1967) samples were routinely taken to provide estimates of water potential and stomatal aperture. These data were correlated with cuvette and meteorological data collected during each trial. Sampling was carried out at cuvette level and illustrative values reported here represent averages—two to three twigs for Scholander pressures (P_s) and five to seven needles for stomatal infiltration pressure (P_{stom}).

During preliminary trials, the cuvette temperature was maintained within at least $\pm 1.5^\circ\text{C}$ of ambient under conditions of high

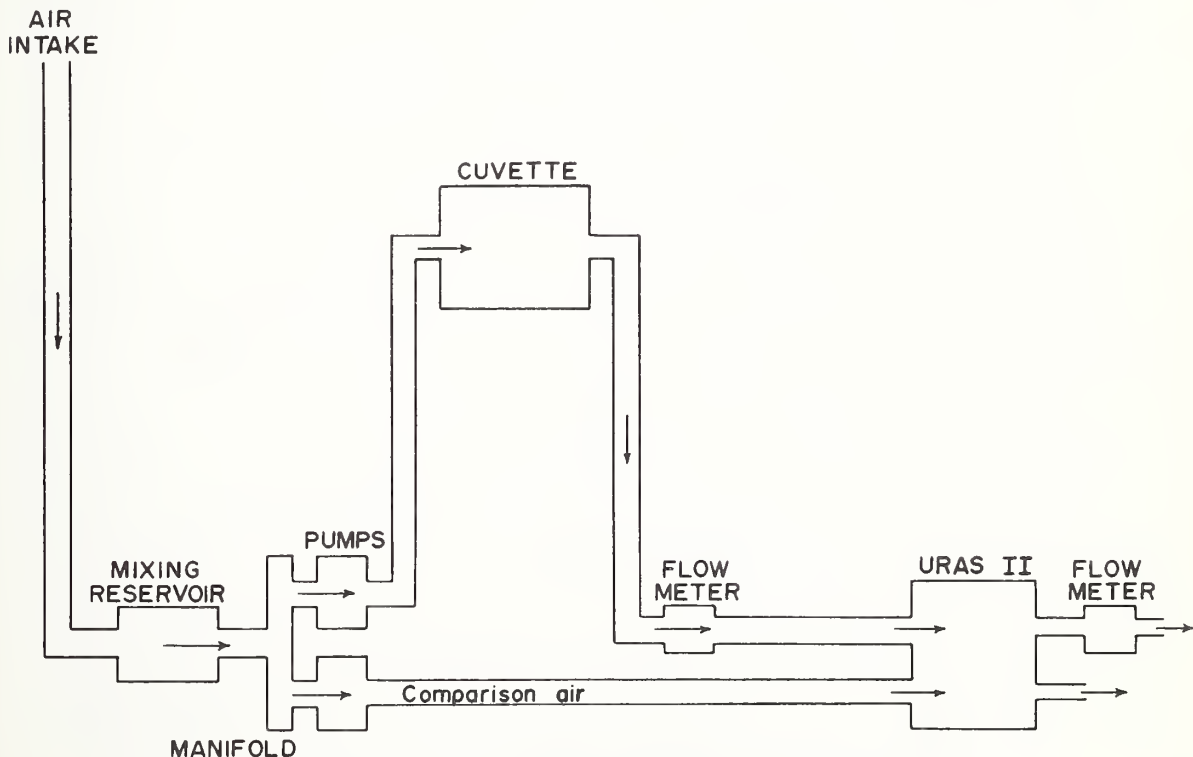


Figure 2. Experimental system used during 1971 field trials.

insolation ($1 \text{ cal cm}^{-2} \text{ min}^{-1}$) and generally control was within $\pm 1^\circ \text{C}$. With the recent installation of aluminum heat sinks on the cuvette floor, incorporation of "sensistor" (Texas Instruments) temperature sensors, and additional electronic balancing of the system, improvement of this performance is anticipated.

Representative Experimental Results

Summer data obtained with the prototype system agree with those of other investigators in suggesting a close relationship between assimilation, stress, and stomatal behavior. To illustrate this, results of a single day's run have been included (fig. 3).

On August 3 and other clear days sampled, light did not appear to limit photosynthesis; maximum assimilation rates occurred between 1030 and 1130 hours (PST); CO_2 uptake

decreased between 1130 and 1230 but was accompanied by continued stress increase and only small changes in stomatal aperture; varying degrees of afternoon stomatal closure followed and coincided with further depression of assimilation and relief of stress.

Acknowledgments

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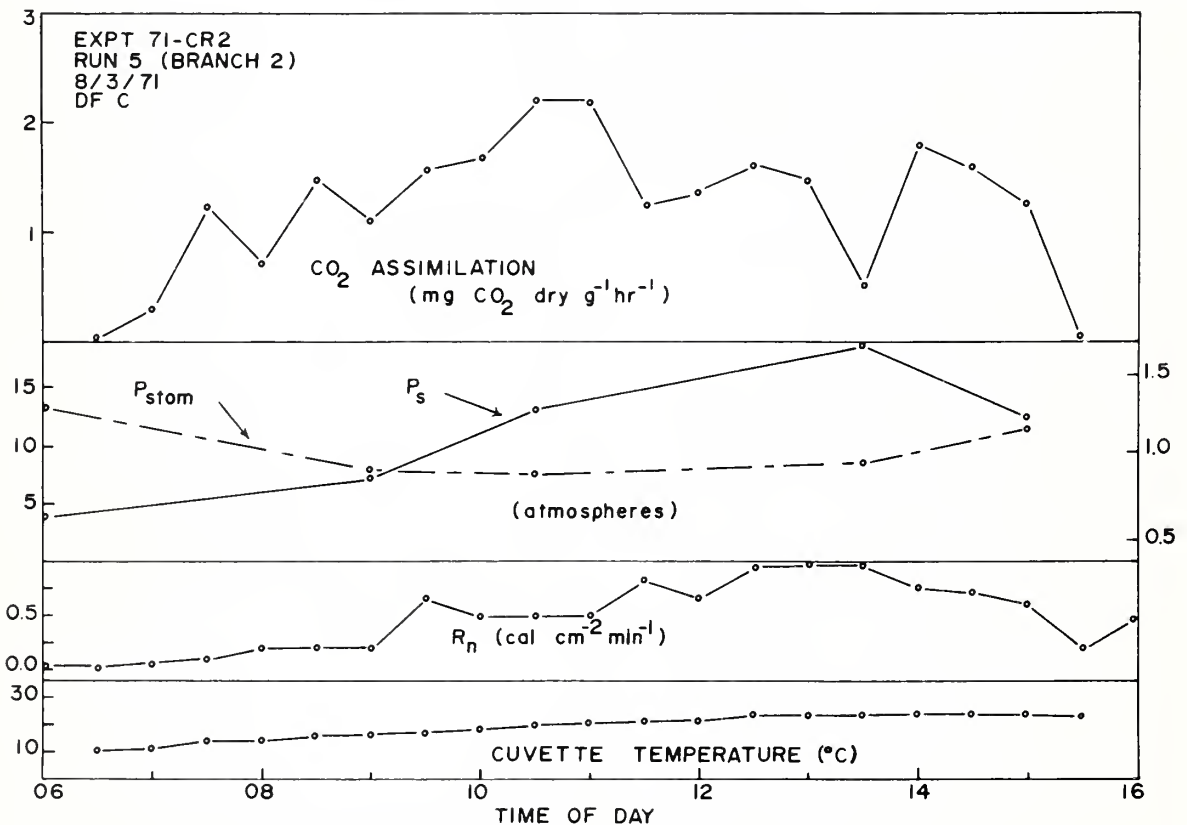


Figure 3. Representative data obtained during cuvette field trials.

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Aquatic Process Studies

Studying streams as a biological unit

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Abstract

The case for viewing and studying streams from the standpoint of processors of materials and energy instead of exporters from the forest is elaborated. The unique opportunity for stream and terrestrial biogeochemical investigators to cooperate and be coinvestigators on the same stream systems is explored and specific programs are identified.

The shift in emphasis from standing crop sampling and instantaneous ingestion and growth information to process studies utilizing radioisotope material balance experiments and carbon flux experiments is explained. Short term experiments using radioisotopes as food markers are described and discussed as to their usefulness in determining the effect of food quality on ingestion rates and assimilation efficiencies.

The Stream as a Biological Unit

The primary aquatic interface with the terrestrial component occurs in small watershed streams. There is a general consensus that the stream itself probably contributes little to the conservation of nutrients (compared to the total terrestrial system of which they are a part) since relative biomass levels are low and export is a pervasive feature of streams, particularly during freshets. Such ideas, although partially correct, have helped to perpetuate out-moded views advanced by terrestrial ecologists around the turn of the century concerning streams. The opening paragraph of a paper by Shelford and Eddy (1929)¹ is sadly appropriate in 1972:

Modern ecologists . . . have considered that the development of communities gives the clue to their dynamics and relations to each other. Most plant ecologists have usually assumed that there are no permanent fresh water communities. This assumption is based upon negative evidence. Streams change their locations, and it is essentially their abandoned posi-

tions that become ponds and develop into land communities. Streams are permanent as long as the existing climate endures, and this is the condition under which land communities reach a climax.

The state of the art of stream ecology has clearly upheld Shelford and Eddy's hypotheses that permanent stream communities exist, undergo successional development, reach and maintain a relatively stable condition, and manifest seasonal and annual differences, i.e., streams are bona fide biological units. To continue further, streams are highly evolved biological units. As Hynes (1970) has pointed out, almost every taxonomic group of invertebrates is represented in, on or near the substratum of lotic environments. In contrast to lakes and ponds there are several groups which occur only in lotic systems and more which reach their maximum development and diversity there. This is quite probably a consequence of the permanence of streams as compared with lakes and ponds. Rivers rarely disappear so they are not evolutionary traps (Hynes 1970).

The attitudes of terrestrial ecologists toward streams have not basically changed since the paper of Shelford and Eddy (see footnote 1). A recent symposium at Oregon State University on forest land uses and

¹ V. E. Shelford and S. Eddy. Methods for the study of stream communities. *Ecology* 10: 382-392, 1929.

stream environments (Krygier and Hall 1971) indicates that attitudes toward streams by policymakers and foresters may be changing. However, with the notable exceptions of Chapman (1966) and Lantz and Hall (personal communication), the analysis of the effects of logging on streams seldom considers the stream directly from a biological point of view.

In perhaps the most complete study on a watershed to date, the Hubbard Brook Experimental Forest in New Hampshire (Likens et al. 1970, Bormann et al. 1969), the capacity for streams to alter and process the various kinds and forms of chemicals was not considered. The various forms in which nitrogen enters a stream (organic, both dissolved and particulate, and inorganic) and their fates have not been carefully explored for either undisturbed or clearcut watersheds. One might expect that more nitrogen is lost to the terrestrial portion but retained in the stream portion of the forest ecosystem than Likens and Bormann have shown. Indeed, Fisher (1970), working on the same watershed, has shown that 80 percent or more of the particulate fraction that enters a small stream is processed in the stream. Kaushik and Hynes (1971) and Triska (1969), in studies on the fate and residence times for leaves in streams, also indicate that processing and not export is the dominant process.

Objectives of the Research on Andrews Watershed Streams

The inclusion of streams in the Coniferous Biome Study represents a unique opportunity for stream biologists and terrestrial biogeochemical investigators to cooperate on and investigate the same stream systems, thus exploring together long neglected problems. We have taken advantage of this opportunity on the Andrews forest streams by emphasizing major terrestrial-aquatic couplings in our stream investigations such as: (1) obtaining estimates of allochthonous inputs and exports both particulate and dissolved; (2) documentation of successional changes in microflora

and the identification of specific metabolic activities carried out during leaf decomposition; (3) determining the significance of root return of nutrients via riparian vegetation with the aid of radioactive isotopes and mass balance experiments; and (4) estimating the importance of fish and amphibians as the top carnivores in some of the small watershed streams.

The long-range objective of the Andrews stream program is to elucidate the role of a stream in the functioning of the watershed ecosystem. The inclusion of fish, which are certainly quantitatively significant in some of the streams, makes it apparent that the other components and their relationships will be defined as well. The determination of how the relationships between productivity and structure at the various trophic levels are altered by various degrees of land use—in this instance, logging—will be a prime objective. Because of the relatively short-term nature of the research, logged vs. unlogged comparisons will be based primarily upon simultaneous observations over a range of conditions rather than on the conventional before-and-after approach. The Andrews forest provides a wide range of conditions from which to sample; including virgin watersheds, watersheds where streambanks have been recently logged, and watersheds where streamside vegetation has grown after past logging. There are obvious problems in this comparative approach. We will have to look at a number of “undisturbed” streams to establish a sort of natural variance in order to distinguish between natural vs. imposed variation.

The Andrews Approach to Stream Studies

At present the emphasis is focused on the role of the biota in the small streams in the Andrews forest. We are presently determining the structure of the stream, its energy sources, and its energy processing components. This descriptive work is both necessary and tedious and will continue into year 3. The methods and approaches being used are standard for

this type of stream work with some modifications to cover the peculiarities of our specific streams.

A significant problem not being dealt with in year 2 is the dimension of the dissolved organic fraction (DOM) and the utilization of that fraction. The DOM from leaf leachate, algal excretion, and soil solution represents a significant organic pool which turns over quite rapidly, even though a large amount of rather refractory matter may be expected. K. W. Cummins (personal communication),² attempting to model woodland streams in a deciduous forest, estimated that about 50 percent of the total DOM input was reflocculated into fine particulate organic matter (FPOM). This occurred by flocculation around air bubbles, colloidal settling, and chemical precipitation. The other half was metabolized by microbes of which he estimated 50 percent passed off as respiratory CO₂ and 50 percent went into production of microbial FPOM. The DOM compartment is a vital coupling between the dynamics of the stream biota and such biome investigations as stream hydrology and biogeochemistry.

Little is known concerning the many changes in quantity and quality of DOM that are produced by the biological processes in and near streams. The functional role of DOM in stream metabolism is also understood poorly and that information which is available is essentially circumstantial. Inferences have been drawn from physiological studies of bacterial and algal cultures under laboratory conditions. Technological difficulties have delayed the transition from laboratory to field investigations.

The approaches planned, to tackle the dynamics of DOM in forest streams, involve an investigation of the processes of microbial decomposition of allochthonous material, measuring the quantity and quality of DOM involved, and examining the fluxing between physical and biotic compartments in and along the streams.

The variety of stream conditions in the

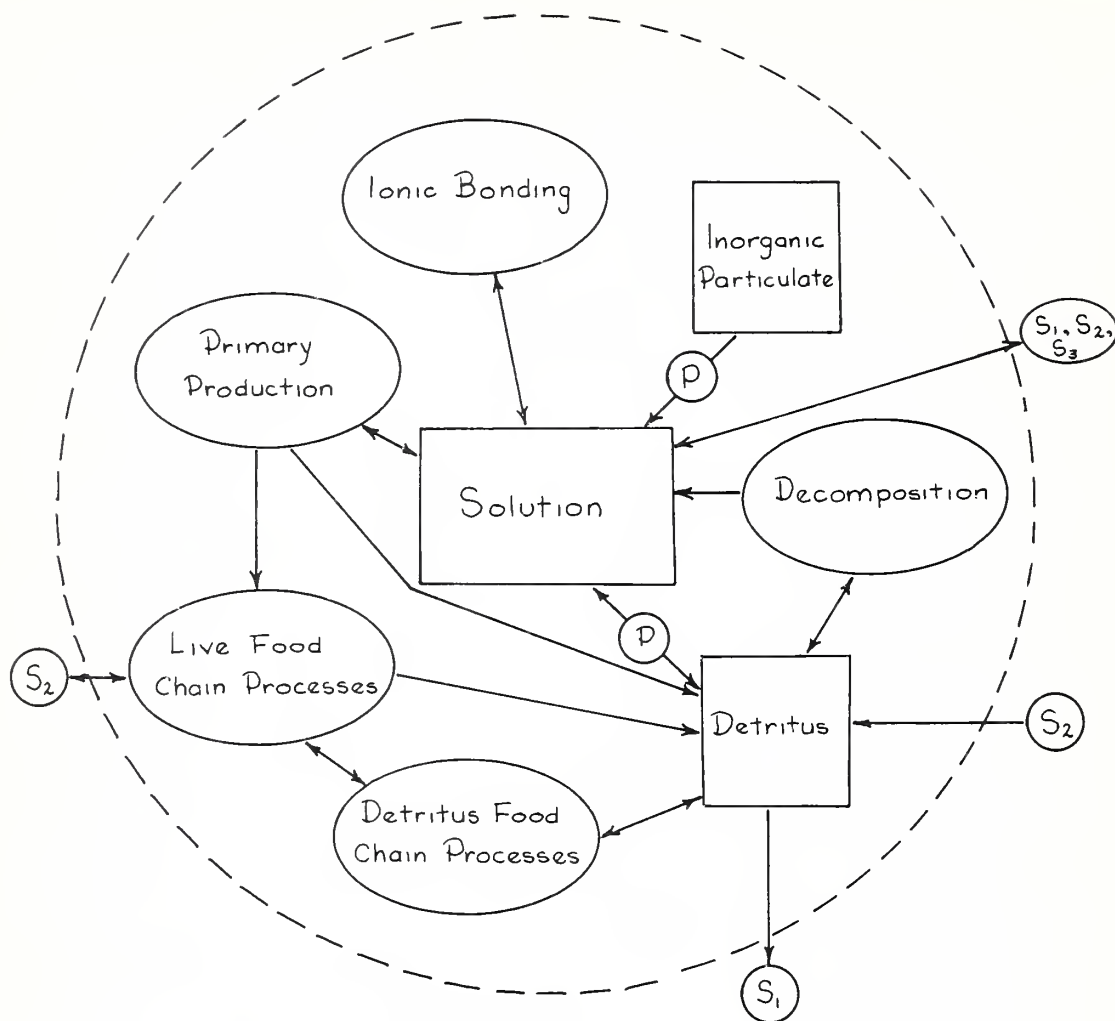
Andrews watersheds provide excellent situations in which to measure the types and amounts of DOM and hopefully develop a budget. Integral to the measurements will be a study of the functional microbial groups involved in the decomposition of the large organic material such as leaves, woody pieces, and fish carcasses. The expertise of an investigator with knowledge of the biochemistry of microbial decomposition will be required.

The necessary techniques for studying stream processes and conceptualizing streams in general have not as yet been adequately developed for coniferous systems. However, major components with the forest stream systems can be identified (fig. 1). Contrary to the opinion of others in the biome, the periphyton and decomposer units can be usefully approached as a "black-box." The complexity can be used advantageously to measure disappearance of substrate and release of products, and some understanding of how ecosystems work and respond to perturbations can be gained. Radioactive isotope experiments will allow us to look at coupled events and processes in the stream. The parameters will be determined by the kinetics of the isotope. We can refine the experiments to look at what features of the system determine these parameters and how. Carbon-14 and phosphorus-32 will be used in mass balance techniques developed by Saunders (1969) and Saunders and Storch (1971) (closed chambers, short-term experiments with C¹⁴) and in situ P³² techniques developed by Nelson et al. (1969) and Elwood and Nelson (personal communication).³ Isotopes of selected elements will be incorporated into biogenic material such as salmon carcasses and the pathways and turnover rates of these elements following decomposition will be investigated.

In addition to the decomposition studies already mentioned, an estimate of the large woody pieces (greater than 1mm) above, in, and near the stream bed will be made. This will be done in cooperation with terrestrial biomass investigations on the Andrews forest.

²K. W. Cummins. Narrative for a stream energy budget model. Unpublished manuscript on file at Kellogg Biological Station, Michigan State University, Hickory Corners. 5 p., 1970.

³J. W. Elwood and D. J. Nelson. Measurement of periphyton production and grazing rates in a stream using a ³²P material balance method. *Oikos* (in press).



S_1 = Hydrologic
 S_2 = Terrestrial
 S_3 = Aquatic
 P = Physical Processes

Figure 1. Stream system categories and relationships.

The primary production and energy sources estimations will utilize the aforementioned P^{32} material balance method. The technique consists of computing a material balance of P^{32} following a 30-60 min pulse release. Total standing crop and effective stream bottom area can be calculated by equating the quantities of P^{32} per unit area of substrate on the stream bottom and per unit weight of periphyton on these substrates to the total quantities of P^{32} retained in the study reach of the stream.

The retained P^{32} in the stream will be subsequently lost in both dissolved and particulate forms through three processes: (1) as P^{32} is replaced by stable phosphorus through metabolic turnover; (2) periphyton containing P^{32} may be sloughed from substrates and transported out of the study reach; and (3) particulate P^{32} released to the stream from primary and secondary consumers and drift of consumers.

Rates of change in the various compartments can be estimated by monitoring the P^{32} in the periphyton and stream water over time. The production rate of periphyton and the grazing rate of periphyton can then be estimated.

Nutrients could be lost from the stream to the riparian portion of the stream study research. The P^{32} technique allows one to measure this movement of nutrients from the aquatic to the terrestrial compartment.

The rationale for carbon flux experiments are discussed in another paper in this symposium by Lighthart and Tiegs (1972). We will not discuss this approach now, except to say that we think the technique can be adapted for use in stream research.

An additional study in the year 3 program will be the role of mosses in the stream bed in fixing energy and cycling nutrients. Their associated invertebrate fauna make them an important compartment in the streams trophic structure.

Studies on the production of benthic invertebrates will be completed. In the analysis of the data particular attention will have to be paid to "strategies of survival" used by the various functional groups of invertebrates. Population regulation must be expected to

differ quite widely in response to the degree of stability of the environment. Freshets in the Andrews forest occur frequently but unpredictably. Food supplies may disappear almost entirely, and animals must be able to withstand and recover from very great fluctuations in numbers. They must be adapted to a great lack of constancy.

Special attention will be paid to the chironomid larvae, pupa and adults. This group which represents the greatest numbers, species and probably biomass of all of the aquatic insect groups, has been somewhat neglected in the first 2 years. Using a foam gathering method the associated exuvia, pupae, and emerging adult midges will be identified and quantified. W. P. Coffman (University of Pittsburgh) will be consulted on the identity of the midges. Feeding experiments with the major invertebrate species will determine ingestion and assimilation rates as affected by the quality and quantity of food.

Meaningful data concerning feeding habits of selected consumers and the relative nutritional values of different constituents of the periphyton are extremely rare. Gut analysis of insects are often misleading as to major source of nutrition due to differential digestion and assimilation rates. Sedell⁴ has reported a technique which allows one to determine if the type of microflora on the natural substrates affect the rates of ingestion of stream invertebrates. Substrates from the stream are either differentially sterilized or are surface sterilized and then reinoculated with an algal, bacterial, or fungal community or any combination of the three treatments. The treated substrate is then soaked for 1 to 3 hours in a stream water solution of Co^{60} . The Co^{60} is adsorbed onto the aufwuchs and the specific activity of the food substance determined (mg/cpm). The Co^{60} is a gamma emitter and can be easily detected without killing the animal. This being the case sensitive experimental designs can be tried which use the individual as a block, thereby eliminating

⁴ J. R. Sedell. Feeding rates and food utilization of stream caddisfly larvae of the genus *Neophylax* (Trichoptera: Limnephilidae) using ^{60}Co and ^{14}C . In D. J. Nelson (ed.), Symposium on radioecology: Proceedings of the Third National Symposium at Oak Ridge, Tenn. May 8-10, 1971. (In press.)

ingestion variation between individuals and ingestion variation between periods. By coupling this method with C^{14} labeling of different compartments of the aufwuchs one can determine assimilation, and the major source of nutrition or at least that food which is most easily assimilated.

Predator-prey experiments have been designed to examine the roles of macroinvertebrates, amphibians, and fish in the stream, and their influence on the community composition and numbers of aquatic insects. The higher consumer portion of the study will also relate the contribution of allochthonous and autochthonous production to the elaboration of fish flesh and to determine how the relationship may be altered by logging or other land management practices.

The role of amphibians in the consumer dynamics of the stream areas in which they are located is being investigated by a member of the terrestrial consumer group. This effort will strengthen the aquatic-terrestrial coupling studies.

The Andrews stream program for years 3 and 4 will be focused on aquatic-terrestrial couplings. Apart from viewing the stream as receiving the bulk of its energy from forest litter, the extent to which the stream delays the export of minerals and nutrients or may return them to the forest is not known. Stream research during years 3 and 4 will be geared to provide some of these answers.

Acknowledgments

The author and stream program are indebted to J. R. Donaldson who has been a constant source of personal encouragement and an active proponent of a vigorous stream program. Our present stream program is an expansion of one very ably organized over the past 2 years by J. D. Hall. Our approach to studying streams as ecosystems reflects in many ways the ideas of K. W. Cummins, who has followed the program and given generously of his ideas since its inception.

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Biome, U.S. Analysis of Ecosystems, International Biological Program. This is Contribution No. 45 to the Coniferous Forest Biome.

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Exploring the aquatic carbon web

6020
p. 289-300 R.L.

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Abstract

An aquatic carbon web containing the six compartments dissolved inorganic carbon (DIC), phytoplankton, zooplankton, dissolved organic carbon (DOC), detritus, and chemoorganotrophic bacteria is discussed. Tentative methods are presented for measuring the pool size and kinetics about each compartment at one depth in the epi- and hypo-limnions during the four seasons in Lake Washington, Lake Sammamish, Lake Chester Morse, and Lake Findley.

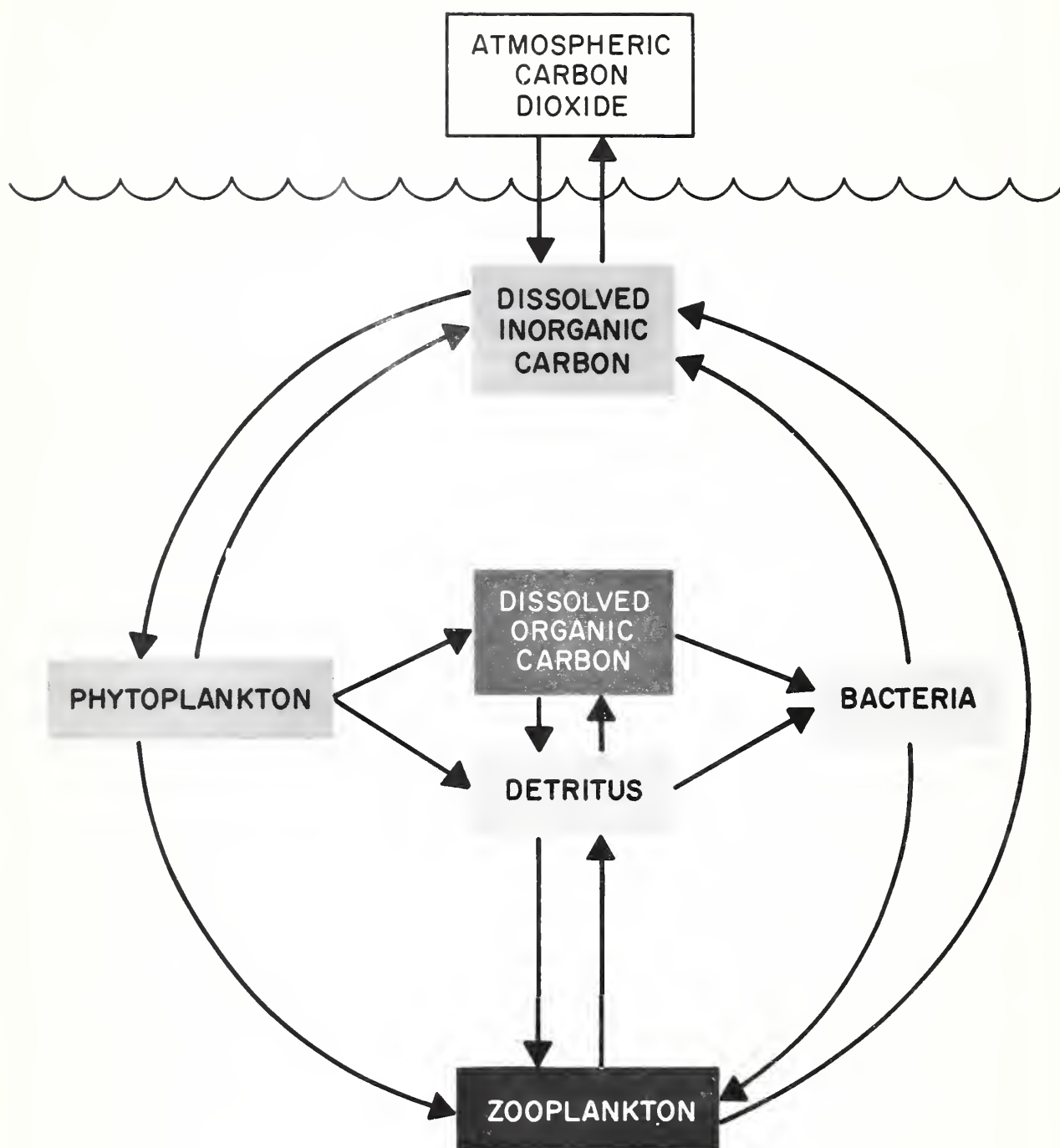
Introduction

It is a primary concern to man to be able to prepare predictive mathematical models of organic forms in aquatic systems if he is going to understand and ultimately develop the tools to wisely manage his water resources. To prepare such models, it is desirable to evaluate the pool size (standing stock) and flux (kinetics) of energy (Lindeman 1942) in all the fractions or compartments of the system. Models may be based on measurements of energy or of several materials, e.g., carbon, phosphorous, and nitrogen; however, both approaches are fraught with technical difficulties. Of the materials named, carbon is recommended because it is a major component of all organic matter and is cycled through a relatively well known web in the biosphere. In addition, it is possible to follow its movement with C^{14} and other simple analytical techniques.

In the aquatic realm, the carbon web may be thought to form a cyclical system made up of a series of interrelated compartments. In this discussion the carbon web will be limited to a consideration of carbon in the following compartments (fig. 1): (1) Dissolved inorganic carbon (DIC), (2) Phytoplankton, (3) Zooplankton, (4) Detritus, (5) Dissolved organic carbon (DOC), and (6) Chemoorganotrophic bacteria (Stanier et al. 1963). The cycle is

initiated when dissolved inorganic carbon species such as bicarbonate (or other chemical species in the aquatic carbonate system (Stumm and Morgan 1970)) are fixed during the photosynthetic process into organic matter by the photosynthetic organism (primarily phytoplankton and secondarily photosynthetic bacteria). Phytoplankton form the first link in the carbon food chain and are either eaten by herbivorous zooplankton, die and become part of the detritus compartment, or excrete dissolved organic carbon (DOC). As much as 80 percent of the algal photosynthate may be excreted as glycolic acid and other compounds into the water (Hutchinson 1957, Fogg 1963, 1965, Hood 1970). Subsequently, microorganisms may take up the DOC transported by the turbulent water and metabolize it to inorganic carbon forms. Saunders (1957, 1971) and Saunders and Storch (1971) have found that the heterotrophic bacteria and phytoplankton form a coupled oscillating pair in which the bacteria increase in activity during the day in response to the daylight production and release of the algal photosynthate into the surrounding waters. The herbivorous zooplankton (and carnivorous zooplankton) also

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contribute to detrital compartment as a result of their fecal deposits or their death and decomposition. Ultimately DOC and detrital carbon are decomposed by bacteria or zooplankton feeding on bacteria/detritus mixtures, to dissolved inorganic carbon as a result of respiratory oxidative decomposition processes.

In nature the standing stock in each compartment is the dynamic equilibrium level attained as a result of input/output rates about the compartment. The quality of the standing stock will also vary as the input/output mechanisms change.

With the advent of the carbon-14 tracer techniques, the transports of carbon to and from each compartment in an aquatic ecosystem is possible. For example, Steemann-Nielsen (1952) initiated such studies with C^{14} bicarbonate to estimate the rate of primary production in the ocean. Goldman (1963) outlined the use of this method in fresh water.

Sorokin (1966), Shuskina and Monakov (1969), and Johannes and Satomi (1967) used labeled phytoplankton to determine the rate at which zooplankton feed and process their waste. The production of dissolved organic carbon (DOC) by phytoplankton (Fogg 1965, Saunders and Storch 1971) and uptake by zooplankton and bacteria have been successfully measured using carbon-14 tracers. Hobbie and Wright (1965) and Wright and Hobbie (1966) refined the enzyme saturation technique of Parson and Strickland (1962) as measured by a carbon-14 tracer, to evaluate the pool size and potential flux of dissolved organics through the bacterial (heterotrophic) compartment in the aquatic web. With carbon-14 labeled detritus Sorokin (1966) measured assimilation by zooplankton. He prepared the detritus by homogenizing radioactively labeled algal cultures. Others have used autoclaved, labeled natural and cultured algal populations² (Bell and Ward 1970). Labeled detritus may also be prepared, by foam separating C-14 labeled dissolved organics from the liquid phase (Baylor and Sutcliffe 1963). However, there is evidence

that this method will work only in sea water.

For the first time, Saunders³ recently combined the aforementioned methods to measure simultaneously all of the previously listed carbon fractions and their fluxes in a "Compartment Analysis" scheme (Patten 1968, Atkins 1969). He has made this type of analysis at one location and one instant in time at several lakes.

Compartment Analysis, in essence, is performed by establishing a series of known fractions or compartments in an experimental confine (e.g., glass carboy or plastic bag) and following a tracer such as carbon-14 as a function of time as it proceeds through each compartment in the confined system. Measurement of the radioactive carbon as it passes through each compartment can be used to evaluate the rate of incorporation of carbon into each compartment in succession, and by isotopic dilution or total carbon content analysis, the pool size estimated. These data may be used to describe mathematically the carbon change in compartments as a function of time, e.g.,

$$\frac{d(q_1)}{dt} = -k_1 q_1 \text{ and}$$

$$\frac{d(q_2)}{dt} = k_1 q_1 - k_2 q_2$$

where q_1 and q_2 are the specific activities of the first and second compartments and k_1 and k_2 are the rate constants into each compartment. The compartments could very well be phytoplankton and zooplankton or DOC, bacteria and zooplankton, etc. The specific activities rather than tracer amounts will be used in mathematical models.

It must be emphasized that the confinement of an aliquot of the sampled water during the compartment analysis will yield values prevailing for (1) standing stock at the time of sample confinement, and (2) uptake values for that particular sample during the incubation period. Thus, it is very important when and where test water samples are chosen. For example, if lake water were collected for a compartment analysis of the carbon fractions during maximum expected respiratory and

² G. W. Saunders, personal communication.

³ Unpublished data.

photosynthetic activity with respect to season, time of day, and depth, one might expect measurements to approach the maximum values that these variables would attain in situ.

Reviews and key papers concerning various aspects of the carbon cycle in the aquatic realm include the following: zooplankton physiology (Corner and Coney 1968), primary productivity (Ryther 1963, Steemann-Nielsen 1963, and Strickland 1965), dissolved organic carbon (Provisoli 1963, Duursma 1965), detritus (Parsons 1963), bacteria (Wood 1965, Brock 1966, and Lighthart 1969), and food chains (Riley 1963). Also some detailed methods are given in IBP Handbooks 12 and 17, Primary Production in Aquatic Environments and Secondary Productivity in Fresh Waters (Edmondson and Winberg 1971).

To this point, the discussion has been with what might be called a primary system, the components in the carbon web. This system is controlled by another [or] secondary system, the physical and chemical environment. Some of the environmental factors operating on the primary system are listed in table 1.

Because factors in the secondary system regulate changes in the primary system, measurements of the primary system may allow us to interpret the major controlling variables of the water bodies.

Table 1.—Some environmental factors operating on the aquatic carbon web

Temperature
Light intensity, quality, and duration
pH
Trace elements
External inputs of organic matter, i.e., nutrients, antibiotics, and growth factors
Phosphorous
Silica
Calcium
Environmental confines
Water circulation

Purpose

It is proposed that, when possible, one station will be occupied on each of four lakes in the Cedar River watershed: Lake Washington, Lake Sammamish, Lake Chester Morse, and Lake Findley, during the four seasons of the year. While occupied, the flux and pool sizes of six carbon compartments will be measured in the epi- and hypo-limnions. The purpose of this investigation is to determine whether the four lakes are distinguishable in terms of the fluxes and pool sizes of the six carbon compartments with the methods outlined below.

Methods

Carbon pools in each compartment will be made by: (1) estimating the protoplasmic carbon pool from cell volume, and (2) from infrared spectrophotometric measurement of oxidized cellular carbon. Carbon flux between compartment pools will be estimated by following the transfer of carbon-14 added to specific compartments.

Carbon Pool Analysis

It is necessary to determine the "cold" carbon pool size, both to evaluate its standing stock, and in calculating specific activities.

Inorganic carbon in the lake water will be measured either by determining the total alkalinity (American Public Health Association 1971), pH, and temperature, and then consulting the appropriate tables (Saunders et al. 1962) for total available inorganic carbon, or by direct measurement using an infrared CO₂ analyzer (Menzel and Vaccaro 1964).

The dissolved organic carbon in the water samples will be determined on the filtrate of a 0.22 μ Millipore filtered sample of the test water using the method of Menzel and Vaccaro (1964). Carbonates will be driven off the filtrate prior to analysis by sparging the phosphoric-acid-acidified filtrate with nitrogen gas.

The carbon content of the planktonic algae will be made either from dry weight estimation by calculation from cell counts and

volume measurement, realizing that the protoplasm has a specific gravity of 1.1, and is 80-percent water, the carbon content is 50 percent of the dry weight (Lund 1965); or by regression with chlorophyll-a measurement (Steemann-Nielsen and Jorgenson 1968); or by both.

$$\text{Algal carbon} = (\text{protoplasmic volume}) \times (\text{protoplasmic specific gravity}) \times (\text{protoplasmic P.C. water content}) \times (\text{P.C. dry weight carbon}) \quad (1)$$

Zooplankton carbon will be measured using the Menzel and Vaccaro (1964) method of individually picked or 150 μ mesh net filtered samples.

Bacterial carbon will be estimated as the product of cell volume (assumed 0.5 X 1 μ) times cell density (1.1) times water content (80 percent) times the dry weight carbon content (50 percent dry weight) of fluorescence (Strugger 1948) phase contrast microscope enumerated cells.

Detritus carbon will be evaluated as the

sum of the bacterial and algal dry weight, and seston ash weights, subtracted from the total seston dry weight. The weight of the total seston will be determined via combustion of quadruplicate 0.8 μ tared glass fiber filtered and dried water samples less zooplankton. It is assumed that 50 percent of the volatile seston is carbon (equation 2).

$$\text{Detritus carbon} = (\text{seston D.W.} - \text{zooplankton}) - (\text{algal D.W.} + \text{bacterial D.W.} + \text{seston ash weight}) \times (\text{P.C. seston D.W. carbon}) \quad (2)$$

Detritus carbon analysis will be attempted by infrared analysis of combusted total seston after the zooplankton have been removed (equation 3).

$$\text{Detritus carbon} = (\text{total seston carbon} - \text{zooplankton}) - (\text{algal carbon} + \text{bacterial carbon}) \quad (3)$$

Carbon Flux Analysis

Carbon flux will be measured as the trans-

Table 2.—List of compartment systems isolated for carbon flux measurements

Bottle	Added tracer	Compartment system
1	NaH ¹⁴ CO ₃	Dissolved inorganic carbon Phytoplankton Dissolved organic carbon
2	C-starch (U ¹⁴) with or without algal hydraulysate	Dissolved organic carbon Bacteria Dissolved inorganic carbon
3	NaH ¹⁴ CO ₃	Dissolved inorganic carbon Phytoplankton Zooplankton
4	Experimentally generated DOC-C ¹⁴	Dissolved organic carbon Bacteria Zooplankton (Dissolved inorganic carbon)?
5	Experimentally generated Detritus-C ¹⁴	Detritus Zooplankton (Dissolved inorganic carbon)?

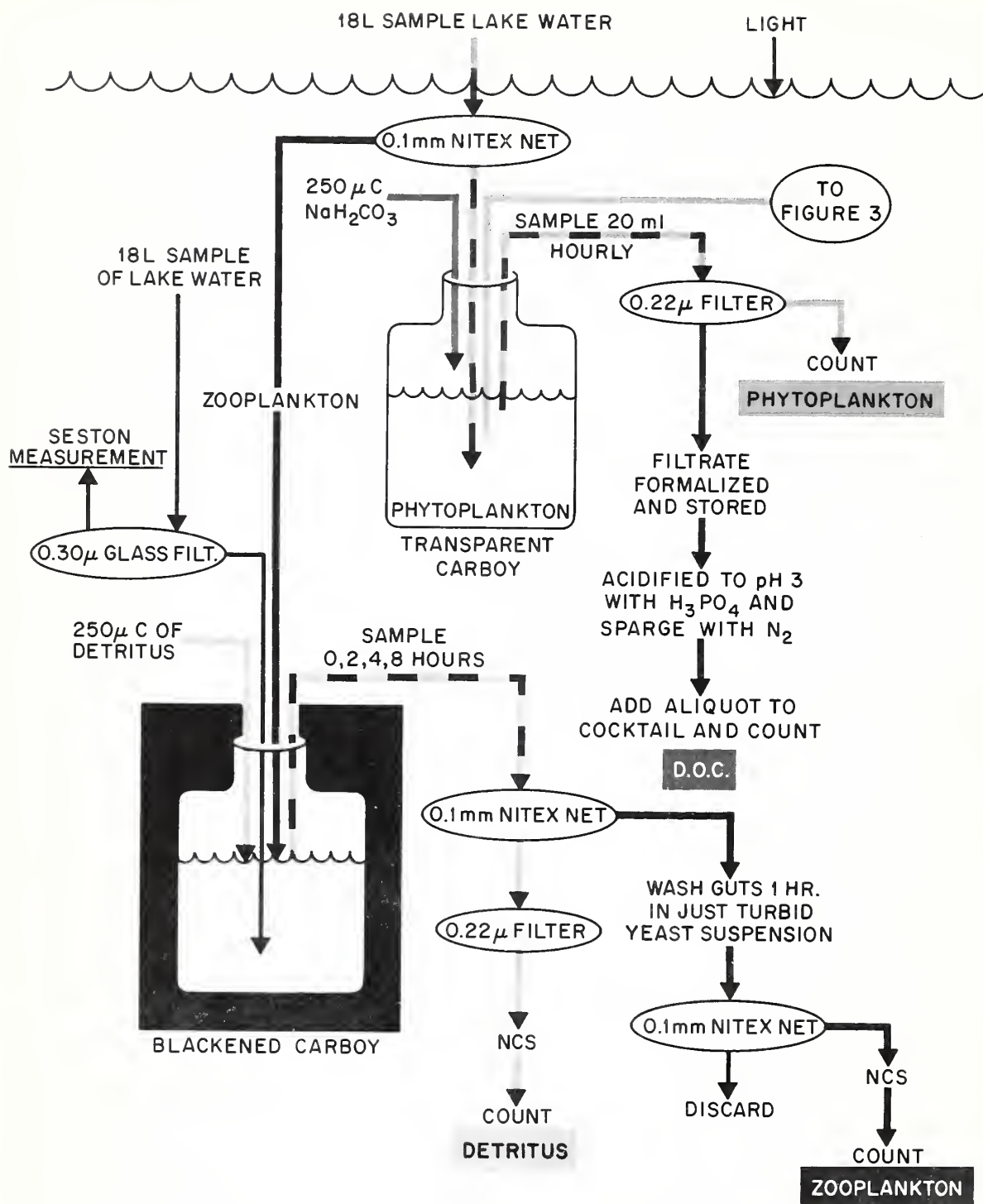


Figure 2. Flow diagram of methods to be used to determine carbon flux from DIC to phytoplankton to DOC, and detritus to zooplankton.

fer of the indicated carbon-14 tracer labeled substrate through the isolated systems tabulated in table 2. Each of the five systems will be isolated in either glass carboys, if it is a light-requiring system, or in blacked plastic collapsible bottles, if a dark system. The bottles will be incubated in situ.

The flux of carbon from DIC to DOC through the phytoplankton will be determined as the uptake during a daylight period of a carbonate spike added to a glass carboy of lake water incubated in situ. The zooplankton will be filtered out of this water with a 0.1 mm mesh Nitex net and used in another experiment. Samples will be withdrawn hourly from the submerged bottle through a tube to the water surface. The Millipore filtered (0.22μ porosity) samples will be used to separate the phytoplankton from the filtrate. The filtrate containing the DOC C^{14} , after acidification and nitrogen sparging, will be dried in a scintillation vial and counted after moistening. Algal respiration will also be evaluated either as the slope of the phytoplankton carbon-14 loss immediately after darkening the bottle, or in separate classical light/dark bottle measurements (fig. 2).

Upon completion of the foregoing experiment, a portion of that carboy of lake water will be used to evaluate the carbon flux from DOC generated by the phytoplankton in it, to DIC via bacteria. This water will be cleared of organism and labeled DIC by first Millipore filtration and then nitrogen sparging. Subsequently, fresh lake water less its zooplankton from the original sample site will be added to the "clean" hot-DOC containing water incubated in situ in the dark. Particulate (i.e., bacteria) and DIC containing activity in the bottle will be monitored for a further 24 hours (fig. 3).

The zooplankton initially filtered from the water for the DIC to algae to DOC experiment (the first experimental description) will be added to a darkened plastic carboy containing sterile radioactive detritus so the carbon flux from the detritus to zooplankton and possibly to DIC compartments may be measured. After 4 and 8 hours, one-half of the carboy will be filtered and the animals counted numerically and radioactively. The

three zooplankton data points so obtained will be graphed to evaluate the uptake rate (fig. 2).

The exact method of sterile detritus production awaits further experimentation to evaluate the chemical composition and optimum zooplankton feeding rate on detritus produced in several ways.

The flux measurement of carbon from phytoplankton to zooplankton will be evaluated in a lighted glass carboy like the one described for DIC to algae to DOC measurements except that the zooplankton will not be removed from the water. Hourly phytoplankton samples, and 4- and 8-hour samples of one-half the vessel will be filtered for subsequent numerical and radiological zooplankton counts. The mean specific activity of the phytoplankton food source for the zooplankton may be evaluated as the mean specific activity of algal carbon during the experiment (fig. 4).

Finally, the flux of dissolved organic carbon through bacteria to zooplankton will be determined as the rate of carbon 14 labeled DOC (i.e., starch and/or C^{14} labeled algal protein hydrollysate) uptake by the bacteria (particles passing through a <0.1 mm Nitex net and zooplankton (particles retained by a >0.1 mm Nitex net) incubated in situ in a darkened plastic carboy of lake water. Samples will be withdrawn hourly for the bacterial-uptake and one-half the carboy filter after 4 and 8 hours for the zooplankton measurements. Zooplankton will be filtered out onto a 0.1-mm mesh Nitex net (fig. 5).

All carbon-14 measurements will be made on a Packard Tri-Carb Model 3375 scintillation counter using the channels' ratio method. Schindler's (1966) method for phytoplankton, and Ward et al.'s (1970) method for zooplankton, detritus, and bacteria will be used. More details of proposed methods may be found in Edmondson and Winberg (1971), and Parsons and Strickland (1965).

The numerical methods that will be used in the analysis of the data generated by this study will be presented in future communications, but are anticipated to include: (a) statistical evaluation of the differences between flow and pool sizes of the biome test lakes as

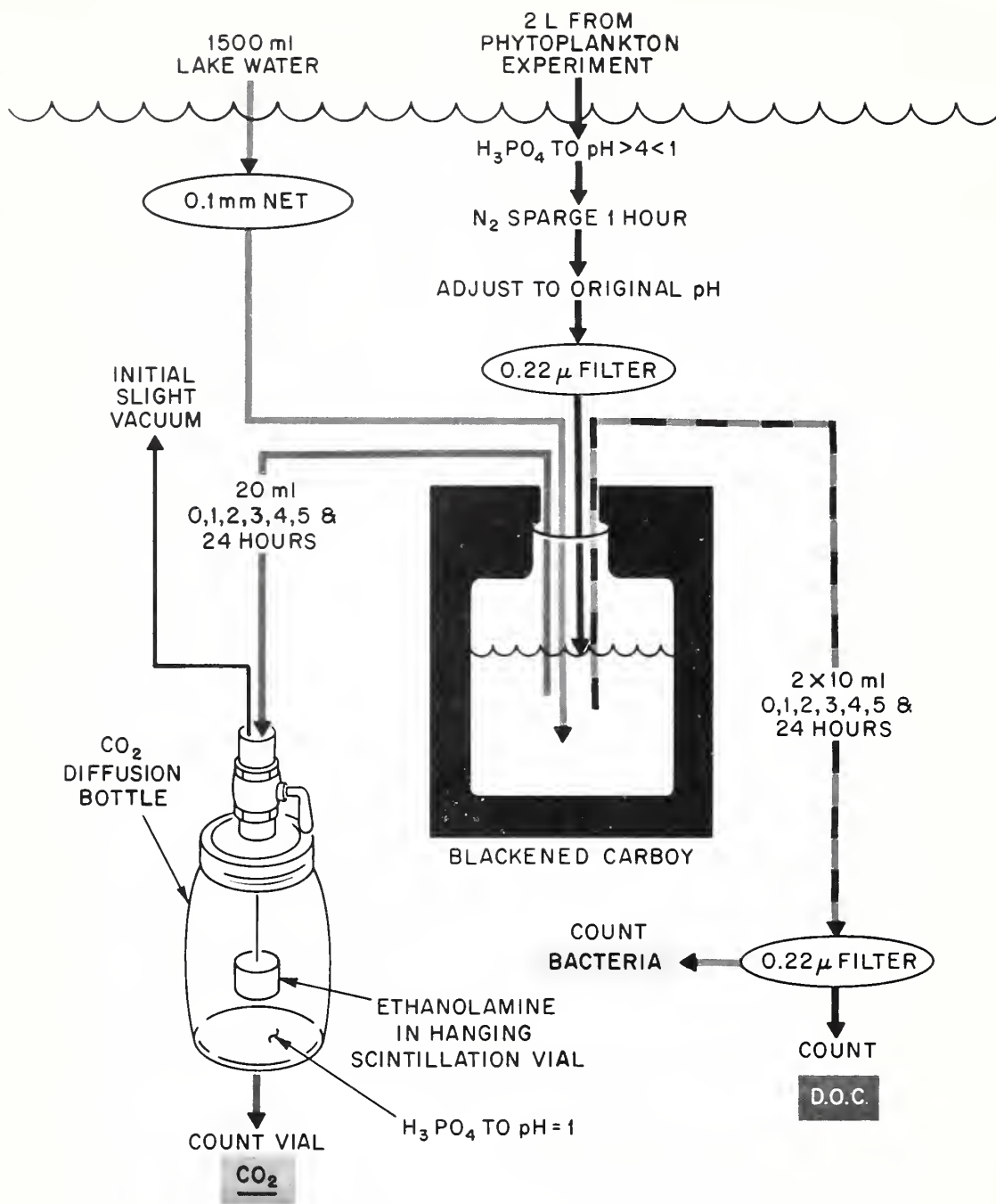


Figure 3. Flow diagram of methods to be used to determine carbon flux from DOC to bacteria to DIC.

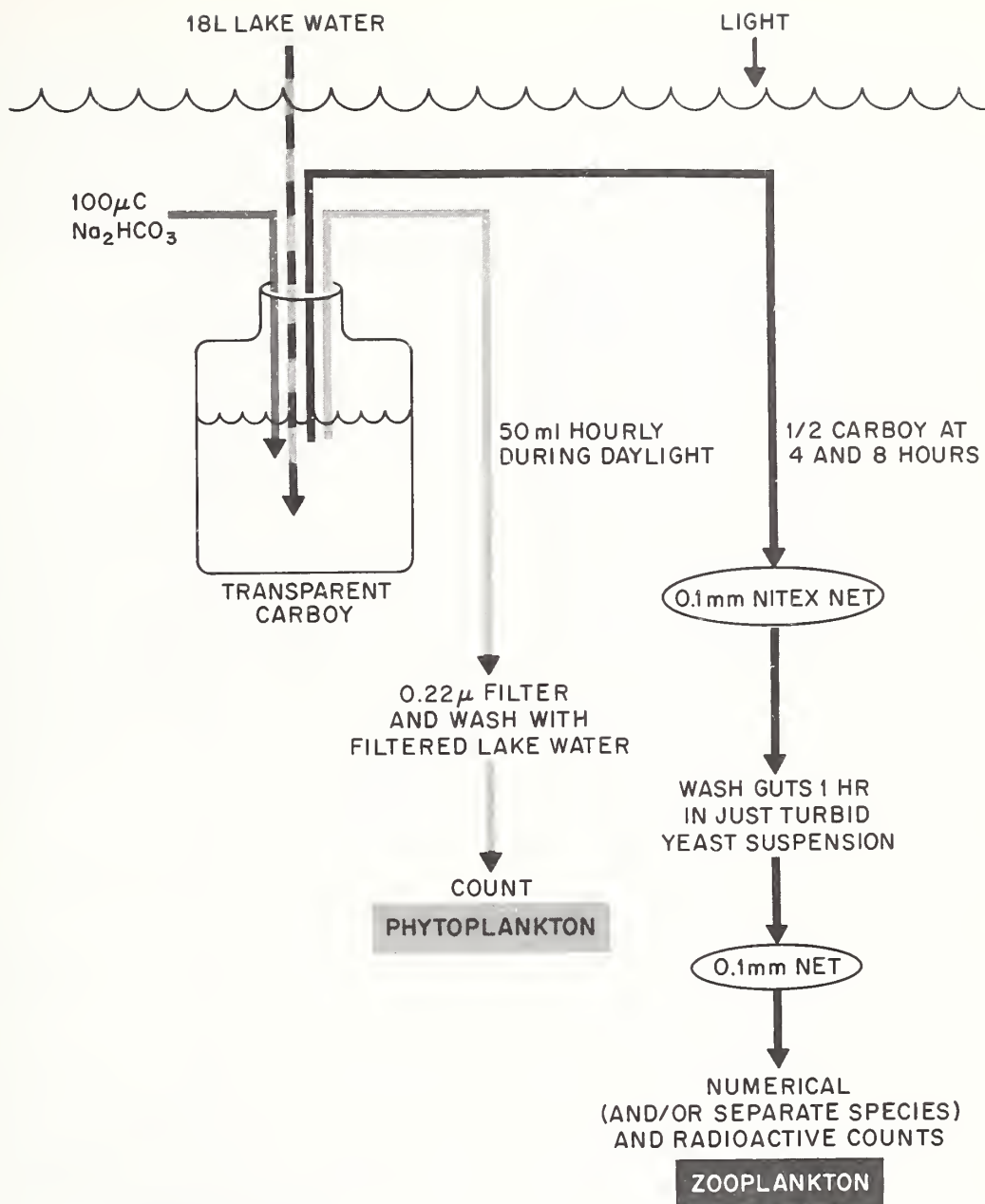


Figure 4. Flow diagram of methods to be used to determine carbon flux from DIC to phytoplankton to zooplankton.

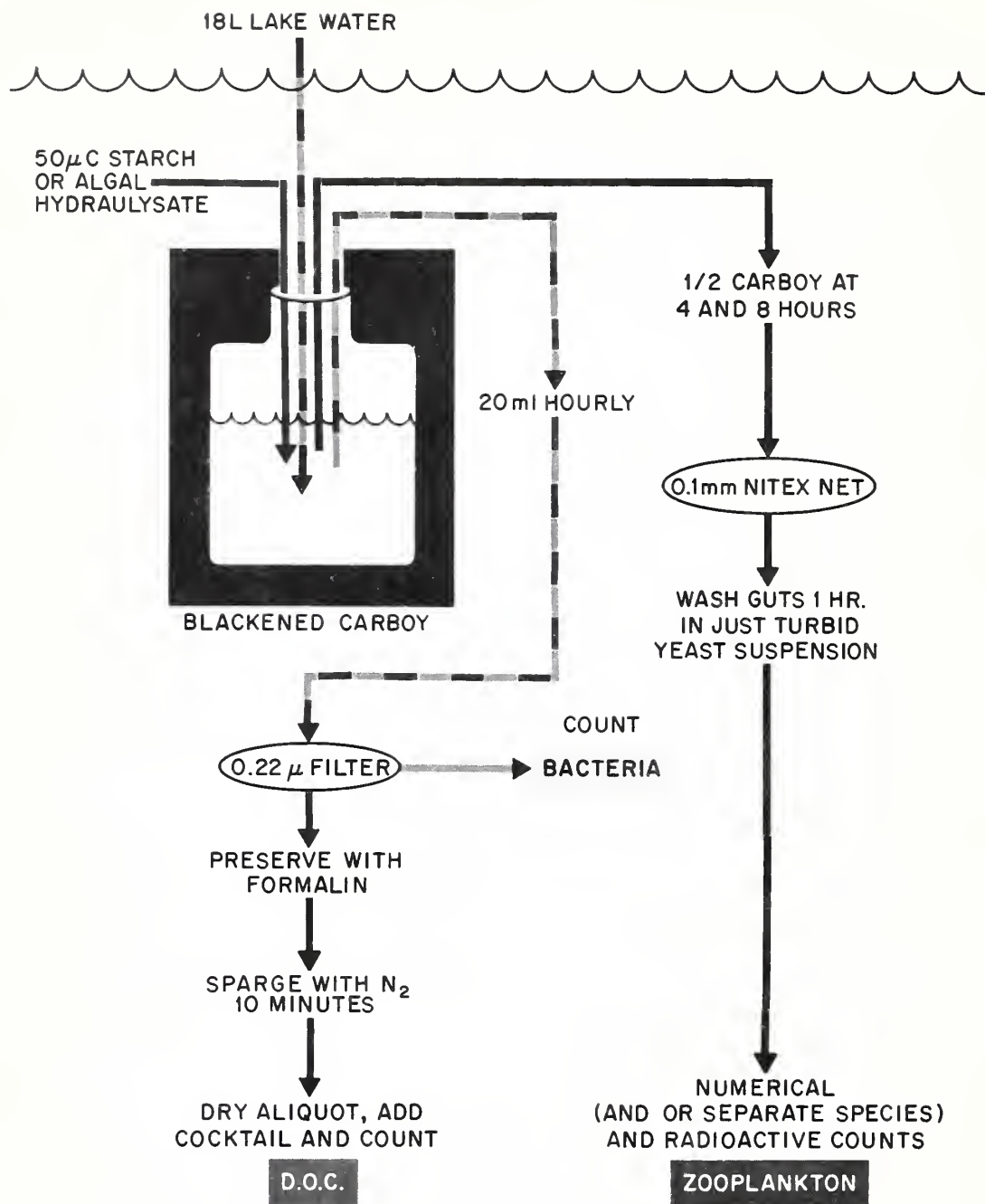


Figure 5. Flow diagram of methods to be used to determine carbon flux from DOC to bacteria to zooplankton.

a function of time and space, (b) carbon balances within the web and between the two test depths station, (c) carbon transfer efficiencies between compartments, (d) synthesis of our data together with other biome measurements that have small time and space resolutions, and (e) carbon flow and pool size input to mathematical models in preparation.

Acknowledgments

The authors want to thank Professor Freida B. Taub for her active encouragement of this study, and Dr. G. W. Saunders, Jr., whose work generated this scheme of methods outlined in this paper.

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Dynamics of nutrient supply and primary production in Lake Sammamish, Washington

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Abstract

Lake Sammamish, which lies about 12 miles east of Seattle, Washington, with moderate depth (mean 17.7 m) and area (19.8 km²), ranks third in productivity of the four Cedar River drainage lakes and can be classified mesotrophic. While diversion of over one-half the P from nearby Lake Washington during 1963-67 was followed by reduction in winter mean P content and a rapid shift from eutrophy to mesotrophy (Edmondson 1970), mean winter P content and measured characteristics of plankton response have not changed in Lake Sammamish following a diversion of similar magnitude. Annual nutrient budgets suggest a reduction in sedimented P since diversion but little change in the quantity of P released from anaerobic sediment. P availability in the water column (winter mean content) appears to be controlled by Fe precipitation to a greater extent than in Lake Washington. Experiments in situ show that N and P are equally limiting to summer phytoplankton productivity, but as found in Lake Washington, P may be of more long-term significance.

Introduction

The supply of limiting nutrient is probably the most significant factor that determines the trophic status of a lake. This relationship can be affected by several factors, particularly those that control nutrient supply such as morphometric and hydrologic conditions. Vollenweider (1968) has related supply of N and P to trophic status of 20 lakes and found that the relationship was dependent on lake morphometry expressed as mean depth. This relationship illustrates that reasonably reliable predictions about the primary production and trophic status of lakes are possible with information on the supply of limiting nutrient and lake morphometry. Such predictability is valuable in the management of man's encroachment on lakes. Of still more value is knowledge of the response rate of trophic status indicators to changes in nutrient

supply.

This paper presents preliminary findings on a nutrient supply budget for Lake Sammamish near Seattle, Washington, and how alteration in that supply by sewage diversion has affected nutrient limitation and primary production. The response in Lake Sammamish to nutrient diversion is compared to that in Lake Washington and mechanisms are hypothesized to explain the delayed recovery in Lake Sammamish. Their trophic status is compared to that of other study lakes in the Cedar River drainage, Findley Lake and Chester Morse Lake, with the ultimate intent of refining predictive relationships among trophic status, nutrient supply and morphometric factors in lakes. Prediction of the rate of response of trophic status indicators to change in nutrient supply should also be enhanced by detailed comparison of manipulated Lakes Sammamish and Washington.

Methods

The water column in Lake Sammamish was sampled at 2-week intervals in spring, summer, and early fall and monthly in winter during 1970 and 1971. Phytoplankton biomass and productivity and nutrient content were determined in samples collected from several depths. Nutrient supply from surface waters was estimated by monthly sample collection and flow measurements from two major and 11 minor streams entering the lake.

Primary productivity was determined in situ according to procedures described by Goldman (1961). Water samples inoculated with C^{14} were incubated at four depths for 4 hours and the results reported as integrated productivity in the photic zone extrapolated to daily rates assuming a 1:1 relationship with incident light. Data are reported from one centrally located station in each of the lakes.

Methods of Strickland and Parsons (1968) were followed for N, P, and Chlorophyll *a* (Chl *a*) analyses in water. Total and orthophosphate phosphorus were determined spectrophotometrically as a phosphomolybdate complex. Reactive silicate was also determined from a silico-molybdate complex. Nitrate and nitrite were determined spectrophotometrically following reduction in a cadmium-copper filled column and are reported together as NO_3-N . Chl *a* was determined with a Turner Model 110 fluorometer. Cations were determined by atomic absorption techniques and anions by routine procedures (American Public Health Association 1971). All analyses except for total P were performed on filtered ($0.45\ \mu$ poresize) water samples.

Surface sediments (surface to 10-cm depth) were collected with a Peterson dredge in the four lakes. Surface sediments in Lake Sammamish were sampled more extensively (26 samples from 26 different depths) than those of the other three lakes where only four to six samples were collected. Analyses for total C, N, and P contents of air-dried sediments were performed with procedures of Baker (1970) for C, Bremner (1960, 1965) for N, and Delfino et al. (1969) for P. The phosphomolybdate-ascorbic acid method of Strickland

and Parsons (1968) was used for the determination of extracted P. Results are expressed on an oven-dried ($104^\circ C$) basis.

Bioassays to determine the limiting nutrient(s) were conducted in large ($0.21\ m^2 \times 5\ m$) plastic cylinders submerged in the lake for 7 days. Nitrogen, P, C, and Si were added to experimental bags separately and in combination. Phytoplankton response was determined by daily measurements of productivity rate and Chl *a* concentration. Significance of response was judged from results of analysis of variance using a factorial design and Dunnett's test at the 95-percent level of confidence (Steel and Torrie 1960). Data are graphed as integrated values over time to indicate total production.

Trophic Status

Lake Sammamish

Lake Sammamish is considered mesotrophic judging from measurements of phytoplankton productivity, biomass (Chl *a*), hypolimnetic oxygen deficit, and concentrations and loading of N and P. Guidelines for these characteristics are suggested in table 1 for judging the trophic status of a lake. With one exception, values for these characteristics in Lake Sammamish fall in between ranges typical of oligotrophy and those of eutrophy. The exception, mean winter ortho PO_4-P , is greater than the level often considered indicative of subsequent summer nuisance algal blooms (Sawyer 1952). Of probably more significance than winter concentration, however, is annual supply of P. In this regard, Lake Sammamish lies clearly between safe and danger limits of eutrophication, here construed to suggest oligotrophy and eutrophy, respectively (Vollenweider 1968).

These ranges of measured characteristics are at best only guidelines for judging the trophic status in lakes. Eutrophication of lakes is a complex process and is affected by climate, basin morphology and soil type. Differences in these factors could lead to considerable inconsistencies in judging trophic status using the limited number of characteristics in table 1. On the other hand, the

Table 1.—Suggested criteria for judging trophic status of temperate lakes and respective values for Lake Sammamish

Item	Oligotrophic	Eutrophic	Lake Sammamish
Chlorophyll <i>a</i> $\mu\text{g/l}^1$ (growth season mean)	0-4	10-100	7.1
Primary productivity ² $\text{mgC/m}^2 \cdot \text{day}$ (growth season mean)	30-300	1,000-3,000	770
Hypolimnetic O_2 deficit ³ in $\text{mg O}_2/\text{cm}^2 \cdot \text{day}$ (mean rate)	<.025	>.055	.053
Ortho $\text{PO}_4\text{-P}$ in $\mu\text{g/l}^4$ (winter mean)	—	>10	12 (total P, 26)
$\text{NO}_3\text{-N}$ in $\mu\text{g/l}^4$ (winter mean)	—	>300	142
Total P annual supply ⁵ in $\text{g/m}^2 \cdot \text{yr}$ for mean depth 17.7 m	<.15	>.26	.20
Total N annual supply ⁵ in $\text{g/m}^2 \cdot \text{yr}$ for mean depth 17.7 m	<2.00	>4.00	3.87

¹ Based on data from several lakes in Canada and United States.

² Modified from Rhode (1969), including data from Schindler and Nighswander (1970).

³ After Mortimer (1941, 1942).

⁴ Modified from Sawyer (1952).

⁵ After Vollenweider (1968).

Table 2.—Comparison of trophic status indicators (May-August means) in Lake Sammamish surface water with other lakes of the Cedar River drainage, Western Coniferous Biome, Washington

Lake	Total P	$\text{PO}_4\text{-P}$	$\text{NO}_3\text{-N}$	Si	Chl <i>a</i>	Productivity	Secchi
	----- $\mu\text{g/l}$ -----					$\text{mg C/m}^2 \cdot \text{day}$	<i>m</i>
Findley ¹	4.9	1.0	3.0	76	0.3	370	15
Chester Morse	5.1	1.0	16.3	373	1.6	520	7.3
Sammamish	48.0	7.0	86.0	1,100	7.1	770	3.5
Washington ²	18.7	1.1	56.5	—	9.5	1,070	2.3

¹ July and August only because of earlier ice over.

² W. T. Edmondson, personal communication.

measurements of algal response and the two most commonly limiting nutrients probably represent a minimum list of variables most pertinent to the eutrophication process. To increase the general value of such guidelines, the data base should be more extensive in addition to including sediment constituents.

Cedar River Drainage Lakes

Comparison of nutrient and plankton characteristics in the four lakes of the study area (table 2) shows that Lake Sammamish is intermediate in trophic status. Data from May to August show Lake Sammamish to be slightly more eutrophic than Lake Washington based on mean nutrient concentrations, but less eutrophic based on algal density and productivity indices. Judging trophic status from nutrient content during the growing season can be misleading. Lake Washington is actually more than twice as enriched as Lake Sammamish based on annual P supply (0.48 versus 0.20 g/m²), which conforms to the differences in productivity.

Of more interest in table 2 than the comparison of Lake Sammamish and Lake Washington is the striking contrast in the total series. Findley Lake is clearly oligotrophic, while Lake Washington near sea level is apparently transitional between mesotrophy and eutrophy. Lake Chester Morse and Lake Sammamish are intermediate in elevation and trophic status, but nearly as widely separated as are Findley and Washington (for other

morphometric data, see Taub et al. 1972). Data from these four lakes alone should provide a substantial framework for prediction of trophic status from lake nutrient supply and morphometry information, which is important to lake management.

The two oligotrophic lakes are also widely different than the mesotrophic lakes in sediment characteristics and ionic composition. Table 3 summarizes data on major chemical ions for the four lakes. A graded sequence in water chemical composition from the lakes in the upper drainage to Lake Washington is readily apparent. A four- to tenfold increase in concentration is observed with most chemical parameters when comparing Findley and Chester Morse Lakes to Lake Sammamish and Lake Washington. These radical differences in chemical quality of the lake waters in the Cedar River Drainage are primarily due to diversified human use and different geologic formation of the lake basins.

Results of analyses for total C, N, and P in samples of surface sediments are presented in table 4. The larger C concentrations and the higher C/N ratios in the sediments of Findley and Chester Morse Lakes when compared with those values in the lakes of lower elevation appear to reflect trophic status and are most probably due to differences in allochthonous and autochthonous inputs. In the two oligotrophic lakes, most of the organic C in sediments is derived from allochthonous sources which are relatively resistant to mineralization, partially as a result of low N availa-

Table 3.—Average summer (1971) chemical ion content in surface waters of Cedar River drainage lakes (Barnes 1972)

Lake	HCO ₃	SO ₄	Cl	Ca	Mg	Na	K	Specific conductance
-----mg/l----- micromhos/cm at 25°C								
Findley	9.8	0.4	0.6	1.1	0.3	0.8	<0.1	21
Chester Morse	10.4	.5	.8	1.5	.4	1.4	<.2	28
Sammamish	41.5	6.9	2.4	7.6	3.0	4.3	<1.0	102
Washington	36.2	7.2	2.8	6.5	3.5	4.7	<1.0	104

Table 4.—Average C, N, and P contents of surface sediments from Cedar River drainage lakes (Bauer 1971, Horton 1972)¹

Lake	C ²	N	P	C/N ratio	N/P ratio
	<i>percent</i>	<i>----- mg/l -----</i>			
Findley	8.98	5.55	1.09	16.18	5.14
Chester Morse	6.12	3.71	1.56	16.41	2.37
Sammamish	5.11	4.82	1.32	10.60	3.65
Washington	4.22	3.71	2.13	11.37	1.74

¹ Values are in terms of oven-dried (104°C) sediment.

² The sediments from all four lakes contain less than 0.1 percent CO₃⁼ - C on an oven-dried basis.

Table 5.—Comparison of nutrient supply in Lakes Sammamish and Washington before and after diversion with special reference to Vollenweider's (1968) nutrient supply limitations with respect to mean depth¹

Item	Lake Sammamish	Lake Washington
Area (km ²)	19.8	87.615
Volume (km ³)	.350	2.884
Maximum depth (m)	31	64
Mean depth (m)	17.7	32.9
Flushing rate (year)	2.2	3.0
Prediversion annual total P supply (kg)	11,160	92,600
Prediversion annual total P supply per surface area (g/m ²)	.56	1.06
Percent total P income diverted	65 ²	55
Postdiversion annual total P supply (kg)	3,906	41,700
Postdiversion annual total P supply per surface area (g/m ²)	.20	.48
Vollenweider's danger limit of P supply for respective mean depth (g/m ²)	.26	.42
Prediversion annual inorg. N supply (kg)	49,100	246,100
Prediversion annual total N supply per surface area (g/m ²) ³	4.96	5.63
Percent inorg. N diverted	22	12
Postdiversion annual inorg. N (NO ₃ -N) supply (kg)	38,298	216,568
Postdiversion annual total N supply per surface area (g/m ²) ³	3.87	4.33
Vollenweider's danger limit of N supply for respective mean depth (g/m ²)	4.00	6.00

¹ Emery, Moon, and Welch, unpublished data.

² Estimated on the basis of population equivalent nutrients diverted and prediversion annual income to the lake.

³ Total N values are estimated by doubling inorg. N values.

bility. Autochthonous sources are more significant in the mesotrophic lakes. The P content of all lake sediments was relatively high, with the highest occurring in Lake Washington. The smaller N/P ratios observed in the sediments of Lake Washington are undoubtedly due to the higher sediment P concentration.

Nutrient Supply and Primary Production

The trophic status of a lake is probably most closely related to the supply of macronutrients N, P and C, which may not be easily indicated by concentration. Although growth rate of phytoplankton is related to the concentration of a limiting nutrient, production is related to the supply rate of that nutrient

(Dugdale 1967). The trophic status in 20 well-known lakes in the world has been related to annual loading of N and P and mean depth (Vollenweider 1968) and with continued refinement such a relationship promises to be even more useful to management. As indicated earlier, Lake Washington is more productive than Lake Sammamish, and this trend correlated with P supply or annual loading, but not growing-season concentrations. Concentrations during complete mixing in the winter more nearly represent available supply than do concentrations during the growing season. Alteration in the nutrient supply should change productivity, but the rate of that change may depend upon physical characteristics of the basin.

Effect of Nutrient Diversion

Sewage was diverted from Lake Washington

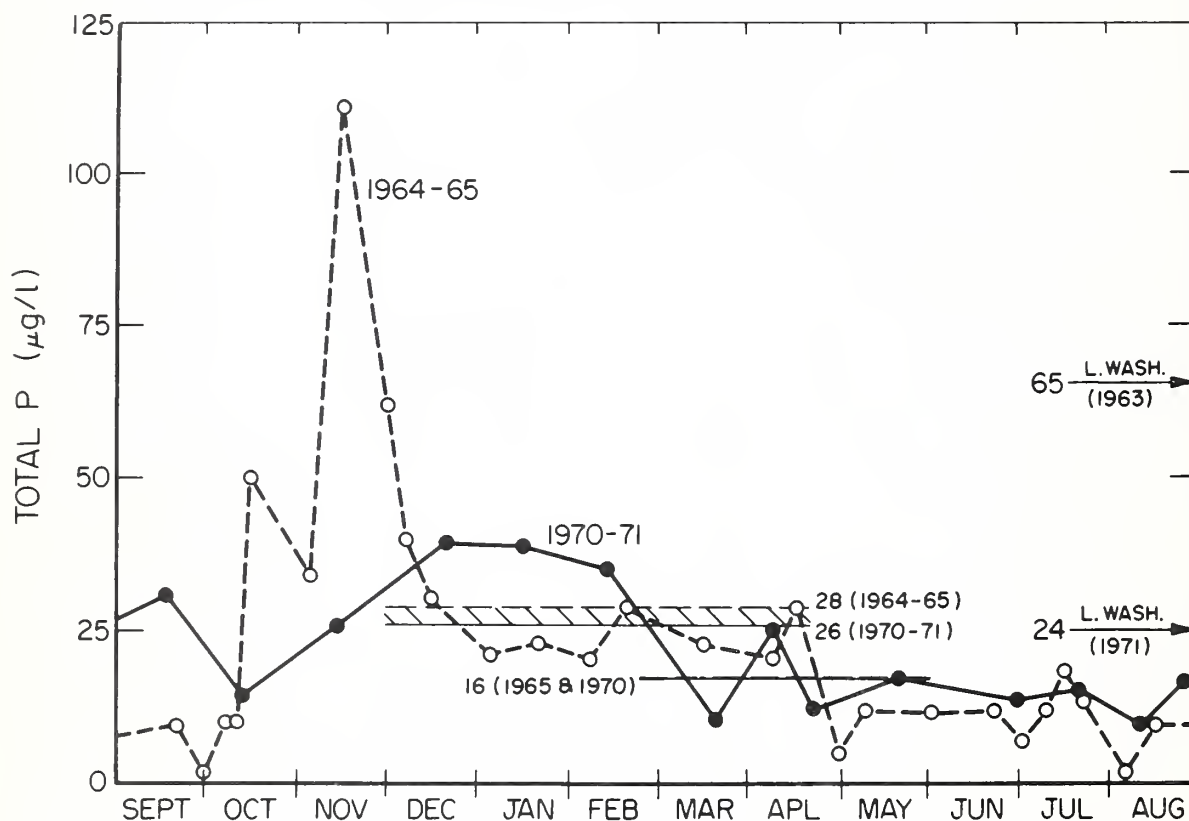


Figure 1. A comparison of surface water total phosphorus for 1964-65 and 1970-71 in Lake Sammamish. Shaded regions represent differences between means for the period covered by the horizontal lines. Arrows to the right indicate winter-spring averages of surface water total phosphorus for Lake Washington for prediversion (1963) and postdiversion (1971) conditions (unpublished data—Emery, Moon, and Welch).

during 1963 to 1967 and from Lake Sammamish in 1968, by the Municipality of Metropolitan Seattle. The diversion removed about 55 percent of the annual external P supply and 12 percent of the inorganic N from Lake Washington. Phosphorus and N external supply into Lake Sammamish was reduced by about 65 and 22 percent, respectively. Although the N supply to Lake Washington is not greatly different than that to Lake Sammamish, Lake Washington received about twice the supply of P than Lake Sammamish (1.06 vs. 0.56 g/m²) before diversion and this difference is still maintained after diversion (0.48 vs. 0.20 g/m²) (table 5). The diversion brought the P supply to Lake Washington to near Vollenweider's danger limit for eutrophication and below the danger limit in Lake Sammamish (table 5). The prediversion N supply did not exceed the danger limit nearly as much as did P in either lake so N diversion may be considered less significant than P. According to the alteration in P supply and if P is most significant in these lakes as Vollenweider's relationship shows, then phytoplankton productivity and biomass should have been reduced in both lakes.

The mean winter (December to April) total P concentration in the surface waters of Lake Washington decreased over 60 percent following sewage diversion (Edmondson 1970). Although diversion was not complete until 1967, winter P concentrations began gradually decreasing soon after the 4-year diversion process was initiated in 1963. In contrast, little difference can be seen in the 1971 winter mean P concentrations in Lake Sammamish 3 years after diversion in 1968 (fig. 1).

Phytoplankton biomass quickly responded to the reduction in mean winter PO₄-P content in Lake Washington as shown by Edmondson (1970) (fig. 2). Chl *a* decreased in direct proportion to PO₄-P, while the other macronutrients, C and N, varied independent of Chl *a*. A significant change in phytoplankton biomass, production or water clarity has not been observed in Lake Sammamish.¹ In

one respect this is gratifying because winter mean NO₃-N and total P concentrations, which should indicate available supply, also have not changed. In another respect, the delayed responses of winter mean P content to diversion of over one-half the annual supply to the lake suggests that factors controlling these winter levels in the two lakes are different in either kind or magnitude.

Factors controlling winter P concentrations in Lake Sammamish are not yet understood, but comparison of seasonal changes in total P and morphological characteristics between the two lakes offers a hypothesis. Winter P content remained high until the spring diatom pulse in Lake Washington following which a moderate decrease was observed (see footnote 1). In Lake Sammamish, total P content normally increased to peaks as high as 70 to 100 µg/l following turnover in November. Instead of remaining high until the spring diatom pulse in April, as it does in Lake Washington, total P decreased during the winter in Lake Sammamish before the diatom pulse (fig. 1). The surface water in Lake Sammamish has been observed to become cloudy with particulate matter during turnover and remain that way for a month or two before clearing. Phosphorus may be sorbed by this particulate matter and removed in shallower Lake Sammamish (mean depth 17.7 m), while in deeper Lake Washington (mean depth 37 m), particulate matter from the bottom is not so readily mixed to the surface. In support of this, iron content during and following turnover is higher in Lake Sammamish than in Lake Washington particularly in the hypolimnion. The lower residual P content in late winter in Lake Sammamish is undoubtedly due to P sedimentation through interaction with relatively greater amounts of iron (Horton 1972, Shapiro et al. 1971).

Recovery rate in Lake Sammamish may be slower than in Lake Washington because the former had never attained the enrichment or productivity level of the latter. Rate of recovery might have also been rapid in Lake Sammamish if prediversion annual supply had been as great as that in Lake Washington. There may exist a control threshold level of P in the lake, above which alteration by manip-

¹R. M. Emery, C. E. Moon, and E. B. Welch, unpublished data.

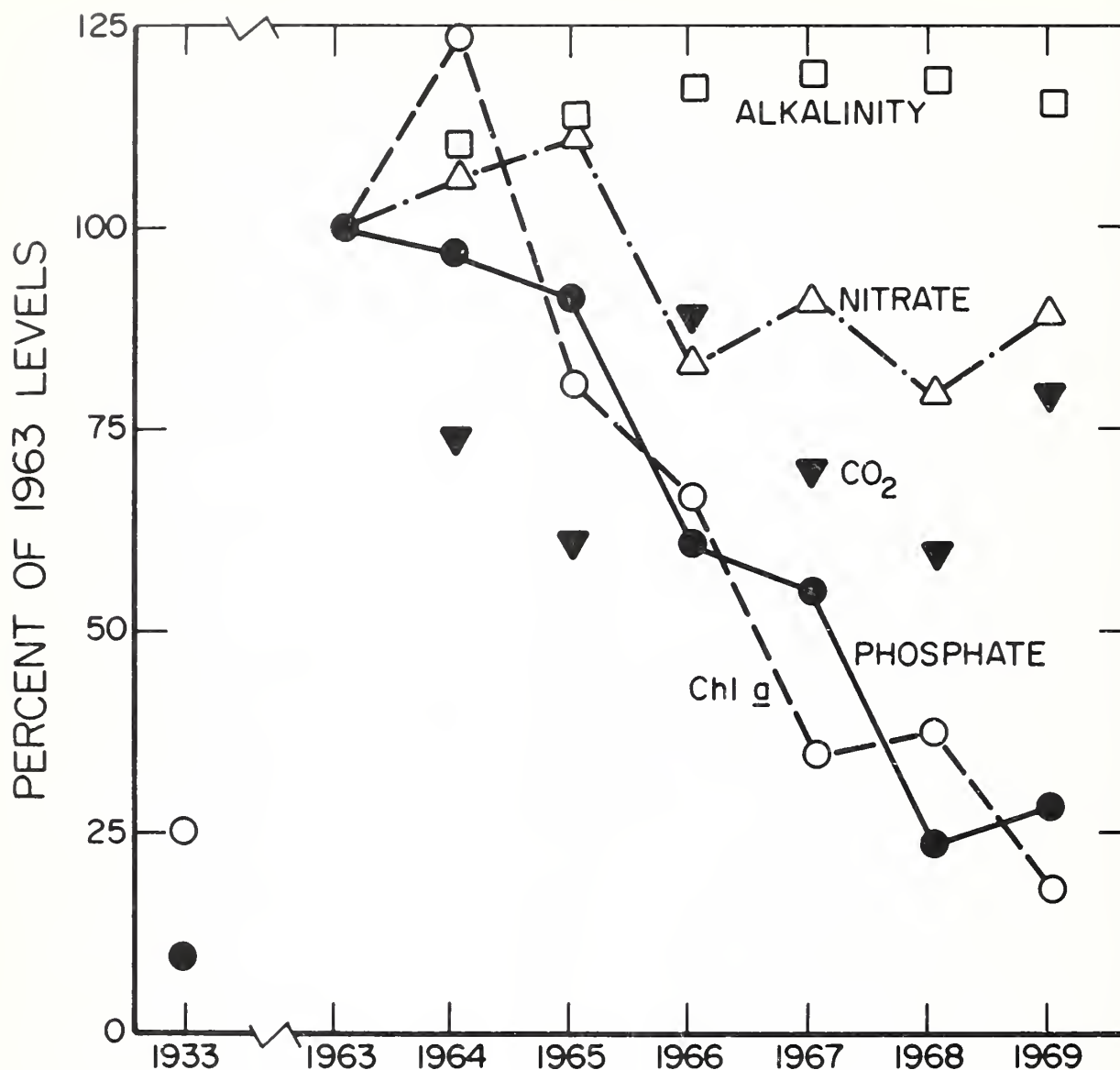


Figure 2. (Printed with permission of W. T. Edmondson and *Science* magazine—Copyright 1970 by the American Association for the Advancement of Science.) Mean winter (Jan. to Apr.) values in surface water; summer (July and Aug.) values of Chl *a* in surface phytoplankton. The 1963 values, plotted as 100 percent, were (in micrograms per liter): P, 57; N, 428; and Chl *a*, 38. Unconnected points show winter means (Jan. and Feb.) of bicarbonate alkalinity and free CO₂ in surface water (25.3 and 3.2 mg/liter in 1963).

ulation of external supply would be relatively rapid while below that level the response would be very slow.

Response to Short-Term Nutrient Change

To relate external nutrient supply rate to production and trophic status in the lake, the nutrient of most significance must be known.

Is phosphorus the most significant nutrient in Lake Sammamish as has been the case in Washington? This problem was approached in two ways: (1) by observing the seasonal change in N/P ratio compared with productivity rate and biomass and (2) in situ experimental addition of macronutrients separately and in combination to plastic bags. Generally speaking, if the ratio of N:P by weight is

greater than 7.2:1 (16:1 by atoms) then P should be limiting further growth and its addition should increase production with the reverse case true for N. If the ratio is around 7.2:1, then both nutrients would be required to increase production. Of course, this can only be approximately true because the atomic ratio of 16N:1P in algal cells is an average and interaction among nutrients may occur such that ratios different than this average may stimulate uptake of one or more nutrients.

Lake Sammamish has one major phytoplankton outburst which occurs in the spring and is dominated by diatoms. In 1970, the outburst occurred during May (fig. 3), which for unknown reasons was about 1 month later than normal. Productivity followed a similar trend as biomass (Chl *a*), but carbon assimilation (productivity) per unit biomass was noticeably greatest prior to the biomass peak. During this outburst, $\text{NO}_3\text{-N}$ decreased by more than 500 $\mu\text{g/l}$ while ortho $\text{PO}_4\text{-P}$ decreased by 8 $\mu\text{g/l}$ at most, a removal ratio of more than 60:1 (fig. 4). If this ratio of removal represents uptake by phytoplankton, which it most likely does, then it is weighted

heavily in favor of N relative to the expected requirements of cells. Inspection of figure 4 suggests that prior to the outburst, P was in shortest supply relative to needs, but afterward, N actually decreased at the surface to a level less than P_i and N should then have been limiting. The great change in N relative to P, if all a result of plankton uptake, suggests that the supply of $\text{PO}_4\text{-P}$ was much greater than indicated by the concentration decrease. This supply could have come from rapid recycling from the particulate phase and, thus, the relatively constant $\text{PO}_4\text{-P}$ content only represented the difference between supply and demand of P.

The change in mean ratio of N:P in the photic zone is compared to surface productivity and biomass in figure 3. Although it is clear from the ratio that P was in shortest supply relative to needs prior to the outburst and that the uptake was still apparently weighted in favor of N, the mean ratio in the photic zone following the outburst remained near the 7.2:1 required value. Thus, if the average values in the photic zone best reflect the consequence of nutrient uptake by plankton, then both N and P would appear almost

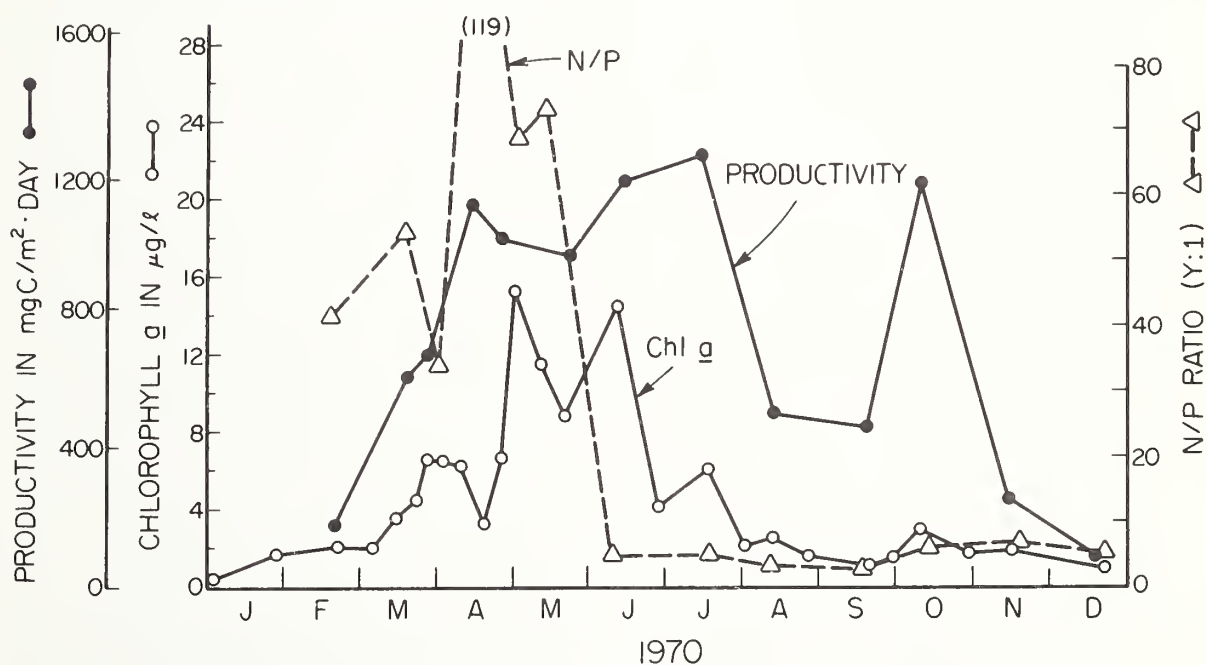


Figure 3. Primary productivity and chlorophyll *a* in the surface water and mean N/P ratio in the photic zone of Lake Sammamish during 1970.

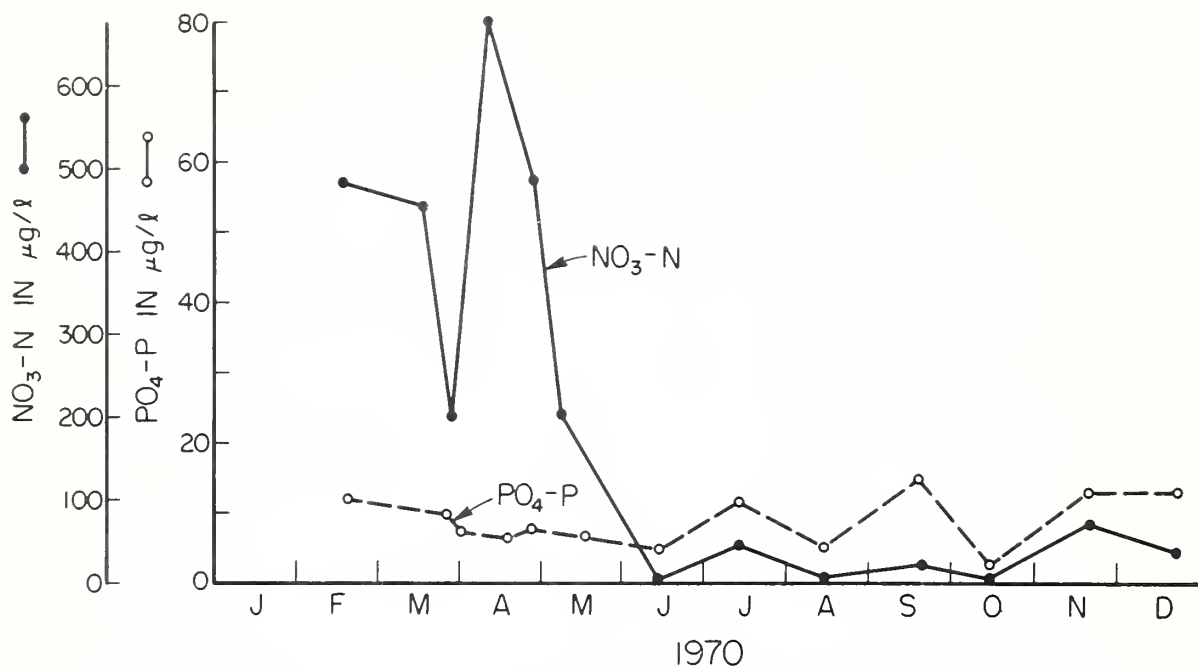


Figure 4. NO₃-N and PO₄-P (ortho) in the surface water of Lake Sammamish during 1970.

equally limiting relative to needs during the summer.

Nutrient limitation was also determined by adding N, P, C, and Si singly and in combination to plastic bags suspended in the lake. Nitrogen and P additions to bags increased the concentrations from a mean of 3 µg/l N and 8 µg/l P to 237 µg/l N and 21 µg/l P, a final ratio of about 11N:1P by weight. Silicon was added as the third macronutrient in 1970 that raised concentrations in the bags from a mean of 0.2 mg/l to 1.3 mg/l, while C was added in 1971 that raised the concentration from 7.5 mg/l to 16.9.

Results of the two experiments are shown in figure 5. Response is measured in terms of Chl *a* averaged over 7 days and C¹⁴ productivity averaged over the first 2 days in 1970 and the first 4 days in 1971. In no case did the single addition of a nutrient significantly stimulate C¹⁴ uptake or biomass accumulation. The phytoplankton response was significantly greater than the control only when N and P were added together. This suggests that the ratio of available N:P prior to addition of N or P must have been near the required ratio of the plankton cells. This is corroborated by

the mean N:P ratio in the photic zone during summer being very close to the 7.2:1 mean considered typical for phytoplankton cells.

Interpretations of limiting nutrients from seasonal data and results of experiments must be used with caution to predict effects of nutrient change in a lake. The conclusion that N and P are equally limiting to phytoplankton in Lake Sammamish as a result of experimental additions is based on measured changes in biomass. This is largely because the response is determined over several days allowing ample time for biomass accumulation. Growth rate may or may not change in response to nutrient addition or change depending upon where the raised limiting nutrient level is on the growth rate—nutrient concentration response curve. However, biomass will respond usually to an increased supply rate of limiting nutrient if other factors are not limiting growth. The change in the N:P ratio is observed after the net result of nutrient uptake and loss has occurred. This can be taken to indicate that an increase or decrease in the supply of limiting nutrient will potentially alter biomass accordingly if other environmental factors are optimum.

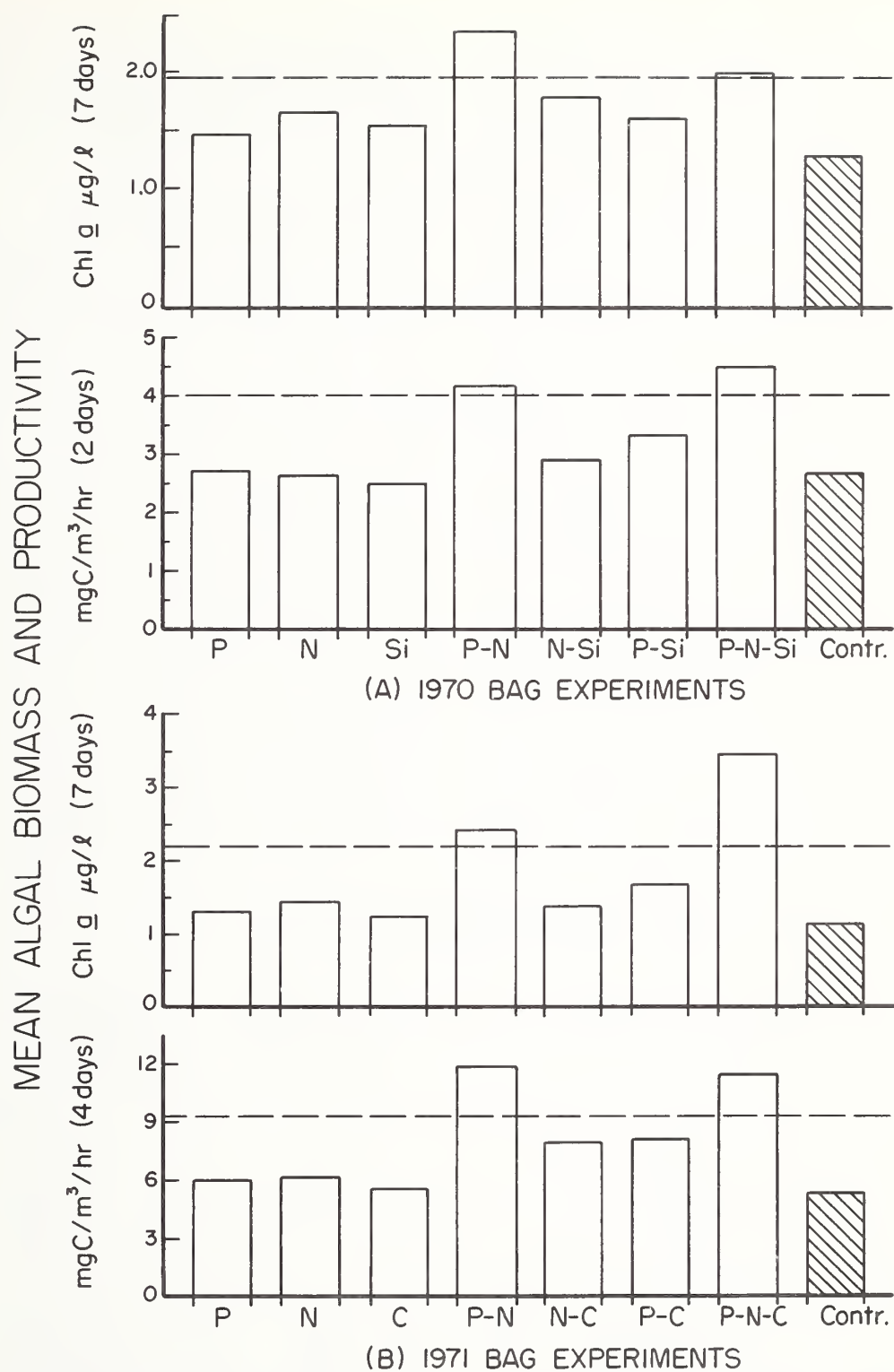


Figure 5. Response of phytoplankton to added nutrients in in situ experiments in Lake Sammamish as measured by C^{14} assimilation and Chl *a* content averaged over time. Significant differences (95-percent level) from the control are indicated by dotted lines (unpublished data—Emery, Moon, and Welch).

As the results of Edmondson (1970) show in figure 2, a continual reduction in winter mean $\text{PO}_4\text{-P}$ content lead to a proportional long-term decrease in mean summer algal biomass. The winter means indicate the supply of nutrient available for subsequent production in summer. This may not mean that in short-term experiments $\text{PO}_4\text{-P}$ was always limiting biomass production. In fact, Edmondson (1970) showed from the N:P ratio in surface water that prior to sewage diversion N was more limiting than P and as P began to decrease more than N, then P became limiting. This indicates that relationships between annual changes in supply of limiting nutrient and mean biomass are more predictable than can be obtained from short-term experiments. Seasonal alterations in the N:P ratio, as occur in Lake Sammamish, can result in different nutrients limiting at different times as a result of interaction between biological uptake and chemical factors. The nutrient that limits most of the time and is, therefore, most influential on lake production can be best indicated from annual data. Although N and P appear equally limiting in Lake Sammamish during August, P supply is considered the most critical factor controlling long-term production as has been the case in Lake Washington. Although plankton biomass in Lake Sam-

mamish has not responded to change in external P supply, the springtime concentration, which also represents supply for summer growth, has also not changed in contrast to the situation in Lake Washington.

Internal-External Nutrient Supply

The internal supply of nutrients, principally from sediments, may also partly explain the slow recovery in Lake Sammamish from diversion of part of the external supply. The total P budget in a 30 m deep water column of Lake Sammamish was calculated for the period of November 15, 1970, to November 19, 1971, as a function of inflow to and outflow from the lake, and of seasonal variation in P concentration in the lake water column (table 6). These calculations were made in a manner similar to those employed by Vollenweider (1968) for data provided by Bachofen (1960) on Lake Baldeggersee. The differences in the values of P concentration in the lake water column at the onset and the end of the stratified period, corrected for external P supply, represent the relative contribution of sedimented P in the water column. The onset of stratification in Lake Sammamish was designated to coincide not with O_2 depletion in the hypolimnion but rather with the first

Table 6.—Exchange of total P between water and deep sediments in Lake Sammamish during one aerobic and one anaerobic period¹

Relative hypolimnion oxygen conditions	Aerobic period, Nov. 15, 1970— May 21, 1971 (188 days)	Anaerobic period, May 21, 1971— Nov. 19, 1971 (182 days)
Change in total P content of representative column of water, g/m^2	-0.870	+1.070
Lake retention from surface loading, g/m^2	+0.134	+0.265
Algebraic difference = amount released by sediments, g/m^2	—	+0.805
or = amount taken up by sediments, g/m^2	-1.004	—
Mean daily rates of release or uptake, g/m^2 day	-0.006	+0.004

¹ From Moon (1972).

detectable increase in concentration of hypolimnetic total P (25-30 m from the lake water surface) over that observed in late spring. Thus, the increase in the hypolimnetic total P concentration from about 15 $\mu\text{g/l}$ in May 1971 to 25 $\mu\text{g/l}$ in June 1971 was taken to indicate the onset of lake stratification. Similarly, the end of lake stratification coincided with the period at which maximum changes in hypolimnetic total P concentration were observed: from about 80 $\mu\text{g/l}$ on November 19, 1971, to 15 $\mu\text{g/l}$ on November 26.

A net P deposition in the sediments of Lake Sammamish is indicated from the data in table 6. For the period of May 21, 1971, to November 19, 1971, P was released by the sediments at a rate of 0.004 $\text{g/m}^2 \cdot \text{day}$. This is nearly three times greater than the corresponding external supply of 0.0015 $\text{g/m}^2 \cdot \text{day}$ for the same period. However, only a portion of the P internal supply from the sediment will find its way to the trophogenic layer of the lake. Normally, most of the sediment-released P will remain locked in the hypolimnion, and enrichment of the epilimnion by sediment phosphorus will depend on eddy diffusion and other mixing mechanisms conditioned by exposure, morphometric, and hydrologic factors; or by the release of gases from the sediments.

It is difficult to appreciate the relative importance of this P internal supply to the trophic dynamics of the water column. Very few exact calculations of phosphorus internal supply have been made that would permit accurate comparisons with these results. Internal P supply from sediments in Lake Baldeggersee, a eutrophic lake in Switzerland, of 0.009 to 0.01 $\text{g/m}^2 \cdot \text{day}$ (Vollenweider 1968) is nearly double that observed in Lake Sammamish. This fact alone, however, cannot be employed to explain differences observed in the trophic status of these two lakes. Sediment P release rates similar to the ones measured in the deep water column of Lake Sammamish would probably have a greater influence on the trophic status of small lakes or, for that matter, the shallow waters of Lake Sammamish. However, preliminary calculations of sediment P released in the shallower (10 m deep) waters of Lake Sammamish,

where oxidized conditions predominate, indicate a P internal supply at least one-half that measured in deep water.

The P uptake by Lake Sammamish sediments during the mixed period (November 15, 1970, to May 21, 1971) was 0.006 $\text{g/m}^2 \cdot \text{day}$. Comparison of Lake Sammamish P budgets before and after sewage diversion indicates a nearly threefold decrease in P uptake by sediments in the period of November to May following autumn lake destratification. More striking than this observation is the fact that the rates of sediment P release for the period of May to November for the years 1964-65 and 1970-71 were identical, 0.004 $\text{g/m}^2 \cdot \text{day}$. This fact will indicate that the mechanism that controls the sediment P release, primarily the anoxic conditions in the hypolimnion, has not changed appreciably following sewage diversion. The prevailing anoxic conditions in Lake Sammamish during late summer and fall bring about large increases in hypolimnetic Fe concentrations (Horton 1972), which upon autumn overturn cause rapid disappearance of P from the water column. Low total Fe concentrations in the hypolimnion of Lake Washington (one-fifth to one-tenth of that in Lake Sammamish²) likely account for the low removal of P from Lake Washington following autumn overturn and maintenance of high winter P concentrations.

In the winter months many more than the monitored 12 small creeks discharge into Lake Sammamish; however, their relative contribution to the P inflow is small when compared to the largest stream, Issaquah Creek, which contributes more than 75 percent and 90 percent of the measured surface P inflow to the lake during the winter and summer months, respectively. Contributions from ground and rainwater, or from direct soil surface runoff, are not included in the calculations presented in table 6. The only surface outflow from Lake Sammamish is through the Sammamish River. Measurements of P outflow from the lake were based on P measurements in that river.

Although the deep water column total P

² W. T. Edmondson, personal communication.

budget in Lake Sammamish indicates a significant release of sediment P to the overlying waters, the relative contribution of internal P supply to the trophogenic layer, when compared to external supply is far from clear. Additional annual P budgets in Lake Sammamish and in other lakes of varying nutrient income, but with similar morphometric and hydrological characteristics, will provide a more accurate delineation of the role of sediments in supplying P to the water column. In particular, measurements of P internal supply for Lake Washington, which is a lake that is morphometrically a macroscale of Lake Sammamish, contains relatively smaller amounts of Fe and P in hypolimnetic waters during the summer stagnation periods, and is more eutrophic than Lake Sammamish, will provide a unique test case. External P supply that remains in the epilimnic and metalimnic layers of Lake Sammamish, at a rate of $0.0015 \text{ g/m}^2 \cdot \text{day}$ during the summer stagnation period, apparently provides a more readily available source of P to the trophogenic layer of the lake than does hypolimnetic P. A more accurate evaluation of the relative importance of internal P supply to Lake Sammamish productivity must await a better understanding of the mixing mechanisms.

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Hydroacoustic assessment of limnetic-feeding fishes

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Abstract

Hydroacoustic techniques have been applied at the University of Washington to determine the number and biomass of limnetic fishes in order to evaluate their role in the productivity of lake systems. The lakes are surveyed with high frequency, high resolution portable echo sounders. The echo signals are recorded on magnetic tape and analyzed by a special computer program. Information on size and species composition is obtained primarily by net sampling, but acoustic determination of size appears feasible in some cases.

Introduction

Determination of the numbers or biomass of fishes has been a continual problem in fishery management. Traditional techniques based on catch-per-unit-effort and tagging experiments have many inadequacies. The problem of assessing fish populations in lake systems is further compounded by the fact that fisheries in lake systems are generally limited, highly selective, or nonexistent, so that catch statistics are of little value.

Determination of the numbers and biomass of limnetic-feeding fishes in lake systems is essential to assess recruitment, growth, mortality rates, distribution patterns and interactions with other trophic levels. As part of International Biological Program studies of the Coniferous Forest Biome at the University of Washington, this problem has been attacked through the application of hydroacoustic assessment techniques.

History of Acoustic Assessment of Fish Populations

Echo sounders have been used since the mid-1930's to study the distribution and relative abundance of fish populations, especially in marine environments. However, prior to about 1960, hydroacoustic studies of fish populations were essentially dependent on subjective interpretation of echogram records. During the last decade, a variety of electronic devices for automated signal processing has been developed. These advances, combined with improved data acquisition systems and increased understanding of acoustic principles, have resulted in a number of successful applications of acoustic techniques to fish population estimations both in marine and fresh waters (Truskanov and Scherbino 1966; Cushing 1968; Thorne 1970; Thorne and

Woodey 1970; Thorne, Reeves, and Millikan 1971; Moose, Thorne, and Nelson 1971).

Acoustic Characteristics of Fish

An echo sounder produces a pulse of sound from its transducer in the form of a spherically spreading cone whose dimensions are dependent on the type and size of the transducer. The distribution of sound energy transmitted in different directions is described by the directivity pattern function and is maximum in the direction perpendicular to the transducer surface, termed the acoustic axis.

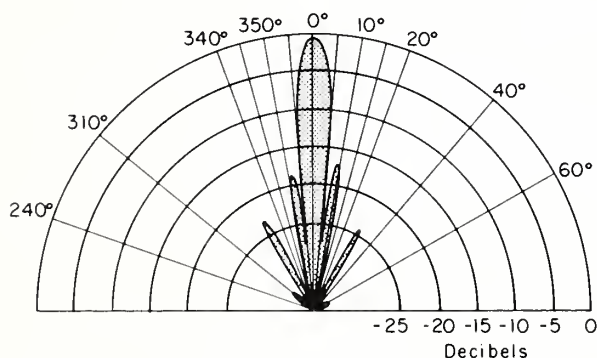


Figure 1. Typical transducer directivity pattern.

An example of a directivity pattern of a transducer is shown in figure 1. A common way to describe the width of a sound beam is to use the half value angle, that is, the angle at which the sound intensity has dropped to one-half (-3 in decibels) of the value it has on the acoustic axis. Since the cross-sectional area of the cone increases with range or depth, the intensity of the sound within the cone correspondingly decreases in proportion to the square of the depth.

When sound is reflected by a fish target, the intensity of the reflected sound is proportional to the incident sound intensity and is dependent on characteristics of the fish target. A measure of the magnitude of the echo from a fish is the target strength, TS, which is defined as

$$TS = 10 \log (I_e/I_i)$$

where I_e is the intensity of the reflected sound measured 1m from the target,

and I_i is the intensity incident on the target.

Investigations into the relationship between target strength and fish size indicate that, in general, the intensity of the echo from a fish is proportional to its weight (Cushing et al. 1963; Shishkova 1964).

Data-Acquisition System

The equipment used on the lake studies at the University of Washington includes an echo sounder incorporated into a system by which target data is recorded on magnetic tape. A block diagram of the system is shown in figure 2. The receiver-transmitter and the chart recorder is a Ross 200A Fineline echo sounder with a frequency of 105 kHz and a transmitted pulse power of about 500 w. A transmitter pulse duration of 0.6 msec is generally used. The receiver amplifier includes a time-varied-gain circuit of $20 \log R$, where R represents depth. This circuit corrects for one way spreading loss of signal intensity with depth.

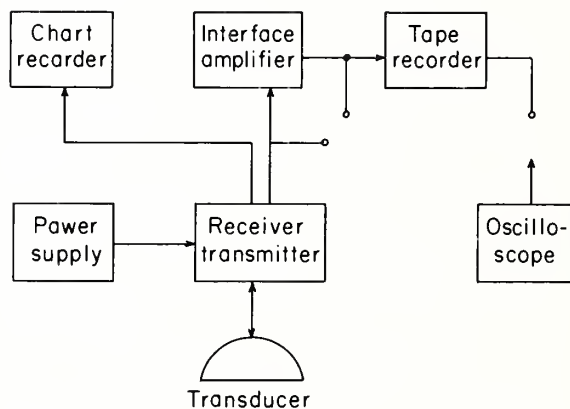


Figure 2. Block diagram of data-acquisition system.

Two modifications of the echo sounder receiver were made so that it could be usable in the data collection system. A transistorized isolation amplifier, which prevents loading of the echo sounder receiver circuitry by associated equipment, was built and installed

within the receiver-transmitter unit. The isolation amplifier couples echo signal data and synchronization pulses to the other components of the system. The second necessary modification to the receiver was the installation of a vernier type control that allows precise adjustment of the receiver gain.

An interface amplifier is used to connect the signal output of the echo sounder to the input of the tape recorder. A direct connection between the two units is not possible because of bandpass limitations of the tape recorder. Target data from the output of the echo sounder are of a 105 kHz frequency, whereas the maximum frequency response of the tape recorder at unity gain is about 8 kHz at a tape speed of 3¾ IPS. The interface amplifier converts the 105 kHz output frequency of the echo sounder to a frequency of 5 kHz by the use of chopper and filter circuits.

The transducer produces about an 8-degree circular beam to the 3dB points. The transducer is generally mounted on a towing vehicle suspended from the side of the boat. The towing vehicle can be used from small outboard vessels as well as large boats, thus allowing complete portability of the system.

Survey Design

Surveys are primarily conducted at night, since most limnetic-feeding fishes exhibit pronounced diel behavior patterns. The fish are generally dispersed in midwater at night but are either on the bottom or schooled in deeper water during the day. The number and spacing of transects depends on the variability of the population and the degree of accuracy required. Studies of optimal survey procedures have not yet been carried out in detail. Transect design, especially in initial surveys, has been governed primarily by the area to be covered and the available time. During surveys of Iliamna Lake, a large sockeye-producing lake in Alaska, transects were spaced about six miles apart, while in Quinault Lake, a small sockeye-producing lake in Washington, transects were spaced about ¾ mile apart. In Lake Washington, where considerable data have been collected, survey coverage is about

one transect per mile. The primary consideration in this design was the number of transects which could be run in a single night. If greater precision is required, the same transects are repeated a second night. During studies of the hake (*Merluccius productus*) population in Port Susan, Washington, we found that about 40 transects with an average length of about 3,500 m over a 45 million m² area were required to produce a precision of about ±15 %, and an additional 40 transects reduced it to ±10 % (Thorne et al. 1971).

Data Analysis

Basic Techniques

Techniques of processing acoustic data for abundance estimation can be broken down into two types: echo counting techniques, which count the numbers of individual targets, and echo integration techniques, which relate fish density to integrated target voltage (Thorne and Lahore 1969). An examination of the theoretical variance associated with the two techniques has been conducted by Moose and Ehrenberg (1971). Principles of echo integration and its application to fish population estimates are described by Thorne (1970, 1971), Thorne and Woodey (1970), and Thorne, Reeves, and Millikan (1971). Echo counting techniques depend on the ability to resolve almost exclusively individual fish targets, thus are limited to relatively low densities. However, echo counting techniques have the advantage that they may also provide data on size distribution of targets. Applications of hydroacoustic techniques to lake systems at the University of Washington have generally included a combination of the two techniques. Basic analysis of data is done by integration, but the integrators are calibrated and size information derived by echo counting.

Echo Counting

Echo counts are made by observation of specific depth intervals on an oscilloscope while the tape recording of a transect is played back. The transecting boat speed and sounder pulse rate are such that nearly all fish

targets are insonified several times. The true number of fish is determined by counting only the peak echo amplitudes from each series of returns from a single fish (corresponding to the location of the fish nearest the acoustic axis). Counting errors are directly proportional to the concentration of fish. When several fish are observed within the counting stratum simultaneously, it is difficult to keep track of the various targets. Under these conditions an alternative counting technique can be used. Instead of counting every fish target, the number of targets within the stratum can be noted for randomly selected pulses, and a mean number of targets per pulse determined for the transect. This number can be directly compared with the sampling volume of the cone to determine the mean density of fish along the transect.

Determination of the Sampling Volume

The sampling volume of the sounder cone can be approximated from the directivity pattern. However, the volume is also dependent on the size and depth of the fish targets, the transmitter power and receiver gain of the sounder and the minimum threshold for counting. The sampling volume can be directly determined from the number of times a target remains within the sounder cone as the boat passes over the fish at a known speed. The width of the path of a fish through the sound cone is determined from the formula

$$w = \frac{\text{boat speed (meters/sec) times duration in cone (pulses)}}{\text{pulse rate of sounder (pulses/sec)}}$$

where duration is the average number of times an individual target is sounded upon. It can be shown mathematically that the average length of parallel chords through a circle is $\pi/4$ times the diameter. Thus the diameter of the sounder cone at the depth of the fish targets is $4/\pi$ times the average path width. The sampling volume of the cone on a single pulse is then the cross-sectional area of the cone (πr^2) at the mean depth times the depth interval. The volume of water surveyed along a transect is the diameter of the sampling cone at the mean depth, times the depth interval times the transect length.

Integration Procedure

Since echo counting from the oscilloscope is time consuming and its application limited to lower density situations, basic data processing is generally done primarily by echo integration. Determination of integrated voltages from the data collected on magnetic tape is done by use of a special integration system utilizing a small general-purpose computer. This system, called the Digital Data Acquisition and Processing System (DDAPS), integrates voltages from fish targets within several depth intervals simultaneously and calculates the fish abundance using input calibration and target strength data (Moose, Green, and Ehrenberg 1971). A block diagram of the system is shown in figure 3. An example of the DDAPS output is shown in figure 4.

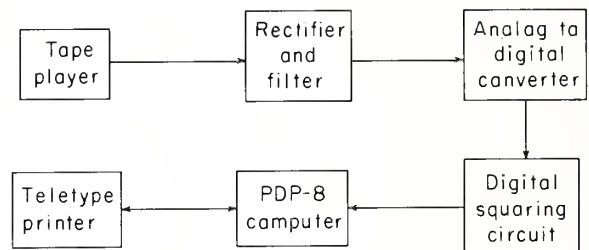


Figure 3. Block diagram of digital data acquisition system (DDAPS).

Upper limit of depth interval	Integrated (voltage) ²	Fish density (N/m ³)	Number of digital samples
6	3485	+0.344950E-04	8181
12	6489	+0.642376E-04	8282
18	38175	+0.377970E-03	8181
24	24162	+0.239227E-03	7154
30	3394	+0.336040E-04	50
36	0	+0.000000E+00	0
42	0	+0.000000E+00	0
48	0	+0.000000E+00	0
54	0	+0.000000E+00	0

Figure 4. Example of DDAPS output.

Typically the average target strength is not known precisely before processing. The density outputs of DDAPS are thus relative rather than absolute. Conversion to absolute density can be made either from measurement of target strengths or by direct comparison of

DDAPS output with determinations of absolute density by echo counting. An example regression of fish density from echo counts and integrated voltage is shown in figure 5.

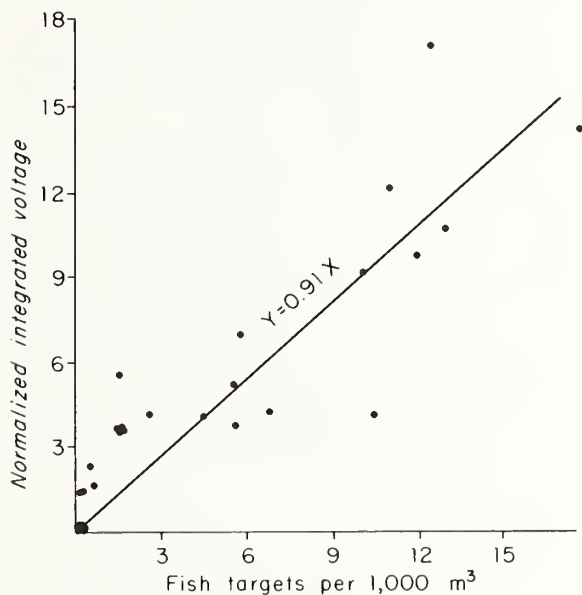


Figure 5. Relationship between integrated voltage and fish density determined from echo counts, Lake Washington, August 1971.

Sampling for Species and Size Composition

The data processing methods described to this point result in absolute estimates of the densities of fish targets within various depth intervals along the various transects. These densities can be extrapolated over the respective volumes represented by the transects to obtain a total estimate of fish within the lake. The species and size composition is not derived directly from the acoustic data and must be obtained from net samples. Several types of nets have been applied at the University of Washington. In Lake Washington, which is accessible by large vessels, a program of sampling with a 10-ft Isaacs-Kidd midwater trawl has been conducted for several years. Development of midwater trawls for use from two outboard vessels is being conducted for lakes not accessible by large vessels. Vertical gill nets of variable mesh size are also being applied.

Size Determination from Acoustic Data

As stated earlier, the target strength of a fish is a function of its size. Thus measurement of the size of the fish echoes gives an indication of the fish size. Unfortunately, the size of the fish echo is also dependent on the orientation of the fish relative to the incident sound (its aspect) and upon its location within the sounder cone. The average effect of the directivity pattern can be sorted out, but, even so, the variability associated with the relationship between echo amplitude and fish size is quite high, and the precision of size determination by acoustic methods is uncertain at this stage. It does seem feasible at least to determine the number of larger fish. Dawson¹ was able to estimate the number of adult sockeye in Lake Washington by counting the large echo targets. The technique probably can be used to determine the number of large fish such as squawfish and peamouth chub in lakes. This ability would be extremely valuable since the large fish are likely to be undersampled by the midwater trawls.

Future Modifications

The basic hydroacoustic techniques for fish population assessment have been derived and are being applied in several lake systems in Washington, British Columbia, and Alaska, including IBP-funded studies of the Coniferous Forest Biome conducted primarily in Lake Washington and Lake Sammamish. Future modifications of the technique will be directed primarily toward refinement of methods of size discrimination from acoustic data, and further automation of data processing. A program for determination of the distribution of target strengths is presently under development with funding from Sea Grant and the National Marine Fisheries Service.

¹J. J. Dawson, Estimation of the 1971 Lake Washington sockeye salmon escapement by means of an echosounder. Informal Progr. Rep. to Wash. State Dep. Fish., Univ. Wash. Fish. Res. Inst., Seattle, 7 p., 1971.

This program will automatically calibrate the integration program to absolute density, thus eliminating the time-consuming echo counting procedure. The data on target strength distribution, compared with the data from net sampling, will provide information on the precision and reliability which can be obtained from acoustic determination of size.

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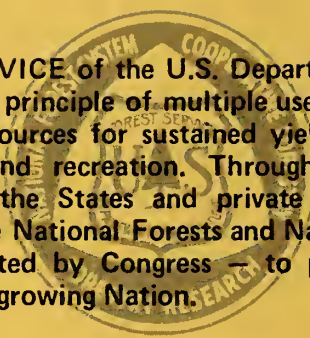
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